L.M.B.C. MEMOIRS.

XXI.

EUPAGURUS.

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Liverpool Marine Biology Committee.

L.M.B.C. MEMOIRS

ON TYPICAL BRITISH MARINE PLANTS & ANIMALS

EDITED BY W. A. HERDMAN, D.Sc., F.R.S.

XXI.

EUPAGURUS

BY

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(With 6 Plates)

PRICE TWO SHILLINGS AND SIXPENCE

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WILLIAMS & NORGATE

FEBRUARY, 1913

EDITOR'S PREFACE.

THE Liverpool Marine Biology Committee was constituted in 1885, with the object of investigating the Fauna and Flora of the Irish Sea.

The dredging, trawling, and other collecting expeditions organised by the Committee have been carried on intermittently since that time, and a considerable amount of material, both published and unpublished, has been accumulated. Twenty-six Annual Reports of the Committee and five volumes dealing with the "Fauna and Flora" have been issued. At an early stage of the investigations it became evident that a Biological Station or Laboratory on the sea-shore nearer the usual collecting grounds than Liverpool would be a material assistance in the work. Consequently the Committee, in 1887, established the Puffin Island Biological Station on the North Coast of Anglesey, and later on, in 1892, moved to the more commodious and accessible Station at Port Erin in the centre of the rich collecting grounds of the south end of the Isle of Man. A larger Biological Station and Fish Hatchery, on a more convenient site at Port Erin, has since been erected, and was opened for work in July, 1902.

In these twenty-six years' experience of a Biological Station, where College students and amateurs form a large proportion of the workers, the want has been frequently felt of a series of detailed descriptions of the structure of certain common typical animals and plants, chosen as representatives of their groups, and dealt with by specialists. The same want has probably been felt in other similar institutions and in many College laboratories.

The objects of the Committee and of the workers at the Biological Station were at first chiefly faunistic and speciographic. The work must necessarily be so when opening up a new district. Some of the workers have published papers on morphological points, or on embry-

ology and observations on life-histories and habits; but the majority of the papers in the volumes on the "Fauna and Flora of Liverpool Bay" have been, as was intended from the first, occupied with the names and characteristics and distribution of the many different kinds of marine plants and animals in our district. And this faunistic work will still go on. It is far from finished, and the Committee hope in the future to add still further to the records of the Fauna and Flora. But the papers in the present series, started in 1899, are quite distinct from these previous publications in name, in treatment, and in purpose. They are called "L.M.B.C. Memoirs," each treats of one type, and they are issued separately as they are ready, and will be obtainable Memoir by Memoir as they appear. It is hoped that such a series of special studies, written by those who are thoroughly familiar with the forms of which they treat, will be found of value by students of Biology in laboratories and in Marine Stations, and will be welcomed by many others working privately at Marine Natural History.

The forms selected are, as far as possible, common L.M.B.C. (Irish Sea) animals and plants of which no adequate account already exists in the text-books. Probably most of the specialists who have taken part in the L.M.B.C. work in the past will prepare accounts of one or more representatives of their groups. The following list shows those who have either performed or promised.

Memoirs from I. to XXI. have now been published. No. XXII., Archidoris, by Miss E. L. Gleave, is far advanced, and will appear next summer.

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ASTERIAS, H. C. Chadwick.
SAGITTA, S. T. Burfield.
BOTRYLLOIDES, W. A. Herdman.

In addition to these, it is hoped that other Memoirs will be arranged for, on suitable types, such as Pontobdella, a Cestode, a Copepod and a Pycnogonid.

W. A. HERDMAN.

University of Liverpool,
January, 1913.

"And I was trimmed in Madam Julia's gown,
Which served me as fit, by all men's judgments,
As if the garment had been made for me:"

Two Gentlemen of Verona, IV: iv.

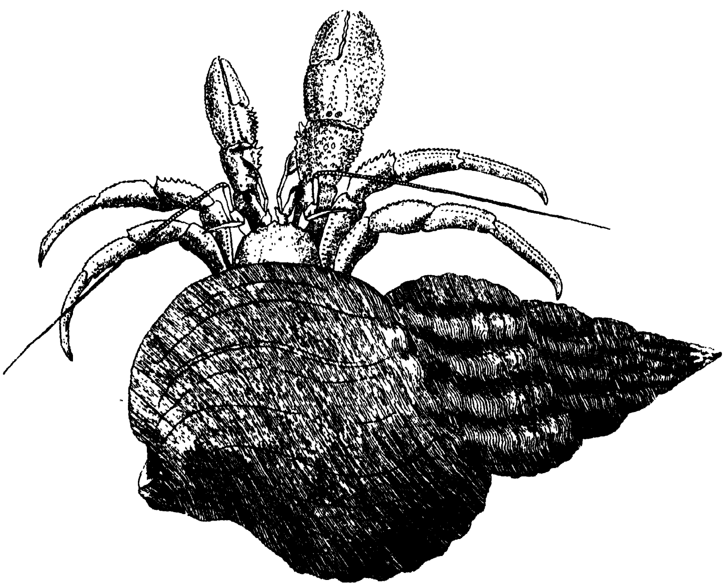
AUTHOR'S PREFACE.

The type dealt with in this Memoir is the common "Soldier" Hermit Crab, *Eupagurus bernhardus*. Points of general Decapod morphology, to which no additions need be made or which have been treated sufficiently in Pearson's "Cancer" (L.M.B.C. Memoirs, No. XVI.), are passed over briefly with references to standard works.

Full descriptions have been given of all matters in which the Hermit-crab stands apart from its fellows, or of any new points of general interest.

I would like especially to acknowledge my indebtedness to Professor Herdman for his supervision of my work and for his careful editing of this Memoir; to Dr. Dakin for his ready advice on all points; and to Mr. Chadwick, of the Port Erin Biological Station, for his ever-courteous response to my requests for material.

H. G. J.



Eupagurus bernhardus, the Hermit Crab, in an empty shell of *Buccinum undatum*.—From a drawing by H. C. Chadwick, A.L.S.

L.M.B.C. MEMOIRS.

No. XXI. EUPAGURUS.

BY

H. G. JACKSON, M.Sc.

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CLASSIFICATION AND DISTRIBUTION.

Eupagurus bernhardus (Linn.) is a Crustacean belonging to the sub-class Malacostraca, the series Eumalacostraca, the division Eucarida, and the order Decapoda.*

The Decapoda may be divided into two sub-orders, the Natantia and Reptantia.† The Reptantia contains four tribes, the Palinura, Astacura, Anomura and Brachyura. The Hermit Crabs are included in the super-family Paguridea of the Anomura, and the following is a detailed statement of the families and sub-families of the Paguridea :—

PYLOCHELIDAE.—Abdomen macrurous and symmetrical with all the limbs present. Trichobranchiate.

COENOBITIDAE.—Abdomen more or less unsym-

* Calman. *Ann. & Mag. Nat. Hist.* Ser. 7, Vol. XIII., 1904.

† Borradaile. ibid., Ser. 7, Vol. XIX., June, 1907.

metrical, some of the limbs lost. Generally phyllo-branchiate. Antennal scale reduced. First antenna with very long stalk and flagella ending bluntly. Land forms.

LITHODIDAE.—Abdomen bent under thorax. Body crab-like. Carapace firm all over. Fourth legs like third. Rostrum spiniform. Sixth abdominal appendages lost.

PAGURIDAE.—Abdomen more or less unsymmetrical, some of the limbs lost, generally phyllo-branchiate. Antennal scale well developed. First antenna with stalk of moderate length and flagella ending in a filament. Marine forms.

Sub-family. *Pagurinae*.—Third maxillipedes approximated at base. Chelipedes equal or sub-equal or the left much larger.

Sub-family. *Eupagurinae*.—Third maxillipedes approximated at base. Right chelipede usually, left never, much the larger.

The Eupagurinae contain eighteen genera, two of which, Eupagurus and Anapagurus, are found in British seas. Of the eleven genera which make up the Pagurinae, *Diogenes pugilator* and *Pagurus fasciatus* have been recorded from English waters; the former is never further north than the English Channel, and the latter is of such doubtful authenticity that it may be ignored.

Of the Eupagurinae six undoubted species of Eupagurus and three of Anapagurus are known.

Anapagurus differs principally from Eupagurus in the possession by the male of a genital appendage on the coxa of the fifth left leg. The portion of the carapace in front of the cervical groove is depressed. There are no other differences which can be put on paper,

although the genera cannot well be confused. The species of Anapagurus at present recorded from British seas may be thus distinguished.*

Anapagurus—

1. Internal antennae, three to four times the length of the eyestalks, which are short and thick. Ambulatory limbs slightly pubescent.—*A. hyndmanni.*

2. Internal antennae about twice as long as eyestalks, longitudinal orange band on hand. Ambulatory limbs almost smooth; a few small spines on anterior borders. Right chelipede of male enormously developed. Row of small spines on wrist of left chela.—*A. laevis.*

3. Internal antennae about three times the length of eyestalks, which are slender. Chelipedes pubescent. Right hand elongate, ovate and smooth, in length equalling the wrist. Left chela slender with nearly parallel sides. Ambulatory limbs smooth, slightly pubescent.—*A. chirocanthus,* Lilljeborg. (*A. ferrugineus*, Henderson).

The key to the British Eupaguridae given below has for its justification the fact that it enables one to identify the living animal, when means of removing it from its shell are not readily available.

Eupagurus—

1. Chelae naked.

(*a*) Limbs tuberculate and spiny on upper border.
Strong rostrum.
Dactyl contorted.
E. bernhardus.

(*b*) Limbs granulate.
Weak rostrum.
Dactyl straight.
E. prideauxii.

* Henderson. *Proc. R. Phys. Soc. Edin.*, vol. IX., 1885-8.

2. Chelae pubescent.

(*a*) Left chela median dorsal carina on hand.

(i) Three long carinae on right hand.

Hand ovate.

Fairly pubescent.

E. excavatus.

(ii) No carinae on right hand.

R. chela wrist = length hand.

Very pubescent.

E. pubescens.

(*b*) Left chela without carina.

(i) Eyestalk longer than A_2 peduncle and little shorter than A_1 peduncle.

Chelipedes densely pubescent.

E. cuanensis.

(ii) Eyestalk as long as A_2 peduncle, but shorter than A_1 peduncle.

R. chela slightly pubescent.

Wrist spiny on inside.

E. forbesii.

The genus Eupagurus is of world-wide distribution. *E. bernhardus* is found in Scandinavian and British seas, Bay of Biscay and Mediterranean. There are doubtful records from the Atlantic shores of North America (probably *E. acadianus*), Behring Strait to Kamtschatka. It seems to be vertically distributed from low-water mark to great depths.

The Paguridea are almost unrepresented in geological strata. Ortmann mentions one species, known by its chelae only, in Hungarian Eocene, but he is somewhat sceptical as to its authenticity. Lörenthey (Math. u. Nat. Ber. Ungarn, Bd. 24, 06) has since recorded three species from Oligocene and Miocene. As in the previous case only the chelae have been found.

EXTERNAL CHARACTERS (Pl. I).

In the segmentation of the body the Hermit Crabs exhibit a wider divergence from what might be assumed to be a typical Higher Crustacean condition than any of their allied Decapods. There is no portion of the body from which a segment could be taken which has not lost its primitive design in its specialisation. In the Macrura and Brachyura the simplicity of the abdominal region is preserved, even if the cephalothorax is specialised, but in Eupagurus the condition of the abdomen is such that it is a matter of some difficulty to demonstrate any segmentation at all. An abdominal segment of the Crayfish (*Astacus*) would be found to possess three kinds of protective plates:—The dorsal *tergum*, the ventral *sternum*, and the two lateral *pleura*. An appendage is attached on each side to the outer end of the sternum. The sternum is attached to its fellows in front and behind by means of a flexible arthrodial membrane, and to each flanking pleuron by a hard membrane—the *epimeron*. No such typically developed segment is to be found on the Hermit Crab. The only fully calcified portions of the abdominal region are the first and last segments, and neither of these is in any way normal. The peduncle never at any stage bears limbs and although a narrow sternum is present in the larva, it vanishes altogether in the adult animal, while the sternum and the pleura of the sixth segment are always in a more or less membranous condition.

Cephalothorax.—The exoskeleton of the Decapoda has been described so frequently that it will be unnecessary to do more than refer briefly to points peculiar to the type under consideration. The first character which calls for mention in the cephalothorax

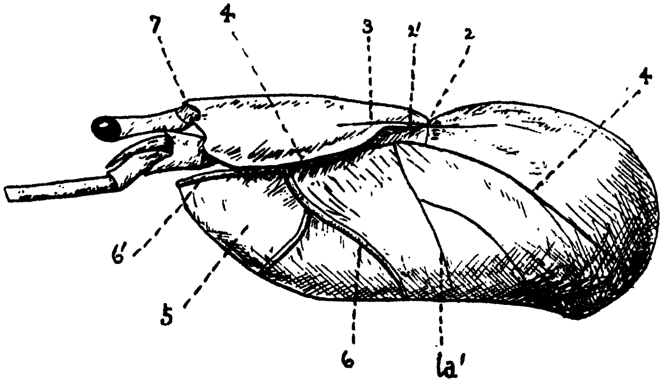
is the slight calcification of the fused terga and pleura. The only portion of the dorsal shield which is at all heavily calcified is the "cephalic" region bounded behind and at the sides by very deep grooves (Text-fig 1). The branchiostegite is almost membranous and the cardiac portion of the carapace is only lightly calcified in its anterior portion. On the anterior border there is a median pointed triangular rostrum of small size, and on either side of it, separated by long shallow excavations, are two supra-orbital prominences.* The front now becomes continuous laterally with deep grooves, which pass back to join the cervical groove. The branchiostegite is hinged to the groove on both sides. It drops vertically downwards anteriorly, almost at right angles to the dorsal shield, but the angle becomes gradually less acute further back, till in the thoracic region the lateral walls form a smooth curve with the dorsal side. Were the body not so narrow, the appendages would present an obstacle to the animal retiring into its shell. As it is, they can be folded up beside the body in a very small space. The proximal joints are flattened considerably from side to side to reduce the size of the animal when it is in its shell.

The lateral border of the cephalothorax is prolonged forwards to form a considerable lobe on either side, which projects on a level with the end of the rostrum. This lobe is supported dorsally by its folded and calcified edge.

The hind border of the carapace is reflexed and attached to the eighth thoracic somite, the tergum of which is partially separate. Certain lines and areas are recognisable on the carapace. The most important of these is the groove corresponding to the cervical groove

* The front between the supra-orbital lobes in *E. prideauxii* is almost linear.

of other Decapods (Branchial groove, Bouvier). It is very deep and is the more clearly outlined by reason of the comparatively dense calcification of the region in front of it. The homologies of the terms by which writers have described the other grooves and lines of the carapace are not altogether clear, but the following account—principally based on Borradaile—summarises the accounts of the various writers.



TEXT-FIG. 1.

Anterior to the cervical groove (c. Boas, c. Bouvier, and 2 and 2′ Borradaile) is a deep longitudinal groove extending forwards to the edge of the front. Bouvier calls this the linea anomurica, and Boas calls it line b. This longitudinal groove is continued as a faint crease to the back of the carapace, and this portion Boas calls the linea anomurica. Borradaile combines the naming of the two others, calling the whole line from end to end the linea anomurica. A small crease (*la′*) passing vertically downwards from this line on a level with the cervical groove is also part of the linea anomurica according to Boas. Bouvier and Borradaile do not recognise it. A small longitudinal groove above the linea anomurica and parallel to it starts from the cervical groove and passes

forward for a short distance. It is called line d by Boas. It, with its continuation backwards past the cervical groove, is probably homologous with the linea thalassinica (line 3 of Borradaile).

For the Text-figure Borradaile's numbering has been adopted (p. 7).* It is as follows:—

2. Boas' line c.—Bouvier's "branchial groove"—commonly known as the cervical groove.

2'. Continuation of cervical groove at the sides of the carapace.

3. Boas' line d. (front part only), also probably the linea thalassinica.

4. Linea anomurica.

5. Soft area at side of carapace.

6. 6'. Borradaile refers to as "hard plates in this area." In this species calcified bars are present which probably represent similar structures.

7. Rostrum.

The **Sterna** of the cephalo-thoracic region do not require detailed description. Those situated posteriorly are mostly very narrow, that of the fourth thoracic somite being reduced to a mere bar in an antero-posterior direction. This sternal bar is in an interesting condition. It is always displaced slightly to the left—a modification due, no doubt, to the asymmetry of the chelipedes and the greater size of the right limb. All the sterna behind the fifth somite are separated by an arthrodial membrane, and the last two are again reduced to narrow bars—transversely placed—separated by long stretches of membrane. The free articulation of the two last segments on one another aids in conforming the animal to the shape of the shell.

* Figure of Callianassa (Fig. 125, p. 691), Gardiner's *Fauna of Maldives and Laccadives*, II., 2. *Marine Crustaceans*, Pts. X and XI.

The **Thoracic epimera** form the inner wall of the branchial chamber and support the gills. The whole constitutes a thin, slightly calcified plate, grooved between the segments by vertical sutures. The inturned edges of the epimera at these grooves form part of the endophragmal system.

The **Abdomen** of the Hermit Crab is quite unique among the Malacostraca. It is a distended sac, which might perhaps be described as banana shaped, into which the gonads, digestive glands and renal bladder have been crammed. The first segment (or peduncle) is small and narrow and calcified. The last segment and its appendages is also calcified, but the remaining four segments are represented by an ungainly membranous bag, which shows practically no trace of division into somites. Traces of the terga can be distinguished above each pleopod on the left side, and in a corresponding position on the right (fig. A, Pl. I). They can barely be seen in young specimens and less in males than females. The position of these remnants shows that the fifth segment is greatly and the fourth rather elongated. Mention should be made of the prominent "columellar" muscle on the third segment. It seems to have only a passive function in fitting the body more closely to the shell.

Appendages (Pl. II).

The appendages of *Eupagurus bernhardus* bear very obvious marks of the asymmetry which affects the whole animal. There is always (in the present species) a striking inequality between the chelae, and of the abdominal appendages only one, the uropod, has survived on the left side. The walking legs, head appendages and maxillipedes remain symmetrical.

A considerable degree of specialisation is shown by the limbs. Some are used for facilitating rapid egress and retreat into the shell, some for locomotory purposes, the telson and uropods for hanging on passively to the shell, and the pleopods for causing a flow of water in the shell, and (in the female) for carrying the developing eggs.

The male and female differ only in the disposition and number of the pleopods. The appendages may be arranged as follows:—

Cephalon.	Somite I.	1st Antennae.
	II.	2nd ,,
	III.	Mandibles.
	IV.	1st Maxillae.
	V.	2nd Maxillae.
Thorax.	Somite VI.	1st Maxillipedes.
	VII.	2nd ,,
	VIII.	3rd ,,
	IX.	1st Pereiopods.
	X.	2nd ,,
	XI.	3rd ,,
	XII.	4th ,,
	XIII.	5th ,,

Abdomen.

FEMALE.

	Right.	*Left.*
Somite XIV.	Absent.	Absent.
XV.	,,	1st Pleopod.
XVI.	,,	2nd ,,
XVII.	,,	3rd ,,
XVIII.	,,	4th ,,
XIX.	Uropod.	Uropod.

	Male.	
	Right.	*Left.*
Somite XIV.	Absent.	Absent.
XV.	,,	,,
XVI.	,,	1st Pleopod.
XVII.	,,	2nd ,,
XVIII.	,,	3rd ,,
XIX.	Uropod.	Uropod.

The **First Antenna** (fig. 1) is attached almost immediately beneath the eye, but the joints turn inwards and upwards, and thus appear to be attached on the inner side of that organ. The ex- and end-opodite, the former of which is much the larger, bear multiarticulate flagella. That on the exopodite possesses a fringe of long setae. The endopodite is quite small and insignificant. In the proximal joint is lodged the auditory sac, which opens to the exterior by a narrow longitudinal slit on the upper side.

The **Second Antenna** (fig. 2) is larger than the first, and considerably more prominent by reason of the very long flagellum. The protopodite is two-jointed and the flagellum—which represents the endopodite—is attached to it by two moveable segments. A narrow pointed sickle-shaped exopodite, the squame, is present.

The **Mandible** (fig. 3) is a strongly calcified elongate structure. The portion immediately under the mouth is tooth-like and strongly grooved within. Into this groove the head of the palp fits. The palp is a little, jointed structure, probably used for cleaning the biting edge of the mandible and helping the food into the oesophagus. The outside portion of the mandible is a long bar (the apophysis), which serves as an attachment for the powerful muscles moving the appendage.

First Maxilla (fig. 4).—Only the endopodite of this appendage is present, and that is a slight structure, bearing a minute flagellum. The coxa and basis, which almost make up the appendage, are membranous in texture but edged with strong setae.

Second Maxilla (fig. 5).—To this mouth-part is attached the Scaphognathite, which represents a modified exopodite. The endopod is a slender spike, partly hidden by the large basis and coxa, which again constitute the greater part of the appendage. Both are unequally bi-lobed.

The **First Maxillipede** (fig. 6) resembles the Maxillae rather than the two following mouth-parts in its general structure. The coxa and basis are still on the inner side, but neither is divided. The rest of the appendage is thin and membranous. The exopod is minute and bears no flagellum; the endopod is more massive and has a fine setose flagellum. There is no epipodite.

The **Second Maxillipede** (fig. 7).—This, and the following appendage, are more or less typical in structure, possessing a seven-jointed endopod, and a flagellated exopod. The exopod in Mxp. II is comparatively much larger than in Mxp. III.

The **Third Maxillipede** (fig. 8).—The basi-ischiopodite bears a row of powerful teeth, increasing in size proximally. The degree of approximation of the two Maxillipedes affords an important point in classification. These two limbs take an active part in feeding.

The **First Pereiopod** or **Chela** (figs. 9 and 10).—In the present type the inequality in point of size of the Chelae is very striking, the right member being half as long again as its fellow. An exopod is absent, two joints, the ischium and basis, are fused and the propos is prolonged forwards to form with the dactylos the crushing edges.

The **Second** and **Third Pereiopods** (fig. 11) are alike. They are similar in essential structure to the Chela, but they are not chelate and the dactylos is long, curved and grooved. It is characteristic of the present species that this joint is contorted.

The **Fourth Pereiopod** (fig. 12) is remarkable for the possession of a moveable dactylos, which forms a sort of sub-chelate termination to the limb. File-like surfaces of corneous granules are present on the propos and dactylos. The last three segments are bent at right angles to the rest of the limb in this and the following appendage.

The **Fifth Pereiopod** (fig. 13) is similar to the previous limb, except in its termination. The last joint is flattened and provided with a stiff brush of setae and a surface of corneous granules. The crab continually passes this leg inside the branchial cavity with a scrubbing motion.

The **Pleopods** (figs. 14 and 15) are essentially the same in structure in both sexes, consisting of a protopodite bearing two rami. They are present in the male on the left side only of the third, fourth and fifth segments, and in the female on the second segment as well. All the male and the fifth female appendages are slender and the internal rami are minute. The other female pleopods (the ovigerous legs) are comparatively massive, and the branches are sub-equal and bear long setae.

Uropods (fig. 16).—The uropods are the only paired abdominal appendages in the adult, and they are the same in both sexes. The external ramus of the left one is large and sickle-shaped, and the whole appendage is much larger than the right one.

Autotomy takes place as readily as in Crabs, and in the same manner. (See "Cancer," p. 56.)

ENDOPHRAGMAL SKELETON (Pl. III).

The Endophragmal Skeleton (figs. 17 and 18) is a complicated system of calcified plates in the thorax, which serves chiefly as an attachment for muscles, but also as a supporting framework for the viscera. It is formed by the inturning of the edges of the epimera and sternum of each segment. Typically two vertical plates arise from the fore and hind border of every thoracic sternum, and a similar plate projects from both edges of the pleuron at the side. Thus each plate is double, as it is duplicated throughout by the neighbouring segments. The outgrowths from the sterna are known as the endosternites, those from the pleura (or epimeral plates) as the endopleurites. The endophragmal skeleton in *E. bernhardus* is not well developed and differs in many respects from that typical of the Macrura. The endosternites are only fully developed in the fifth and sixth thoracic somites. The endopleurites conform more nearly to those of such a type as the Crayfish. A sternal canal is never present. Median plates caused by the folding of the sterna sagitto-longitudinally are developed on the fifth and sixth thoracic segments.

Preparations of the endophragmal skeleton, from which the form of the individual somites may be studied, can be best made in the following way.

Remove all of the carapace behind the cervical groove, separating it carefully from the underlying epimera. Cut off the abdomen at the peduncle, and each limb a few joints from the proximal end. Clean out the gut and stomach, after cutting a window in the cephalic shield, and such portions of the overlying muscle, etc., as can be scraped away without injuring the skeleton, and boil gently for a short time in a 10 per cent. solution of

caustic potash or soda till the skeleton is clean. It may then be washed and transferred to alcohol.

INTEGUMENT.

The structure of the integument of the Hermit Crab does not differ in any respect but degree of calcification from that usually found in the Crabs and Lobsters. Only the chelae and the first two walking legs are comparable with the calcified portions of a Crab in hardness. The rest of the body is covered by a membranous investment with slight deposits of lime in certain places.

The essential structure of the integument is as follows:—*

1. A **chitinous exoskeleton**, which may be shown to consist of four layers.

(*a*) The cuticle, a thin, structureless layer.

(*b*) The pigmented layer, fine lamellae parallel to the surface, between which the pigment lies.

(*c*) The calcified layer makes up the greater part of the hard exoskeleton. It is laminated, but more coarsely than the previous layer.

(*d*) A thin, non-calcified layer.

2. The **epidermis,** which secretes or forms the chitinous layer, and is a single layer of columnar cells.

3. A **connective tissue** or **dermis,** in which are imbedded numerous rosette glands, whose ducts pass through the outer layers to the exterior, blood vessels, muscle fibres and scattered cells.

During *ecdysis* the Hermit Crab follows the same method as that of the Macrura, withdrawing the body first, then the limbs, and lastly the abdomen from the cast-off exoskeleton.

* Vitzou. Récherches sur la structure des téguments. *Arch. de Zool. expér. et gén.*, T. X. (1882), p. 451.

ALIMENTARY CANAL (Pl. III).

As usual in the Arthropoda, three regions of the alimentary canal may be recognised. The fore-gut or stomodaeum—comprising the oesophagus and stomach—which is lined with cuticle; the mid-gut or mesenteron, which is soft-walled and has no chitinous lining; and the hind-gut or proctodaeum—a term synonymous with rectum in this animal—which is also lined with a chitinous cuticle.

Fore-Gut.

The **Mouth** is a laterally ovate aperture lying behind the foot jaws. It is directly covered by the pair of mandibles. In front of the opening—which is directed downwards—is a broad tripartite fleshy lobe, the labrum, and behind it is a smaller lip, the metastoma. The mouth leads directly into the **Oesophagus,** a thick-walled tube whose lumen is greatly constricted by three massive infoldings of the wall (fig. 20). Bright red pigment is always contained in the walls of the oesophagus. Three bunches of stellate glands—two antero-lateral and one posterior—are present at its proximal end, and similar glands are scattered in the lips of the mouth. Each gland is globular, and the somewhat conical cells composing it are radially placed round a small central cavity. From the cavity a narrow duct, which is almost certainly a single cell, leads to the surface. Similar glands occur in large masses in the walls of the rectum. There seems no reason why these glands should have any other function than that of lubricating the walls of the passages in which they are found, in order to facilitate the ingress and expulsion of the food matter. It is difficult to conceive of any

appreciable chemical action being exerted by the oesophageal and labial glands on the lumps of food soaked in sea-water which pass up the tube.

The oesophagus terminates on the underside of the **Stomach** (figs. 21 and 19). Its opening is guarded by a pair of calcified flaps densely fringed with setae. The cardiac portion of the stomach (cardiac fore-gut of Pearson) is considerably larger than the pyloric portion. It is a large membranous bag with a flat roof. The ossicles present in this and the hinder part of the stomach do not diverge sufficiently from the typical form in the Decapod Crustacea to justify a detailed description.* The cardiac ossicle is far more slender than is usual, and is bow-shaped; the pterocardiac ossicles are also slender, and articulate with the long curved zygocardiac bars. The pterocardiac ossicle is almost vertical. Viewed from the side, the oesophageal plates are seen to join the post-pectineal ossicle. Infero-lateral cardiac teeth are present. When the stomach is cut open in sagitto-longitudinal section the general structure of the apparatus can best be seen (fig. 19). The lateral teeth are unusually massive and are prolonged backwards into strongly pectinated ridges. The summit of the cardiopyloric valve also bears a ridge of great blunt setae like a comb. A pectineal tooth is present. There are five valves opening into the intestine, a superior median valve excavated ventrally (fairly large in this species), a pair of dorso-lateral valves and a pair of smaller infero-lateral valves, both richly setose. On the roof of the pyloric region is a pair of semi-circular ridges of setae, and between them a median ridge bears a bunch of setae.

* See Huxley's 'Crayfish,' Pearson's 'Cancer,' Bronn's 'Thierreich,' Bd. V. 2, and many practical text-books.

MID-GUT.

The pyloric valves project into the achitinous **Mesenteron** or **Mid-Gut.** This is by far the largest part of the intestine and measures on the average about 6 cm. in a well-grown specimen. This great stretch of achitinous gut is the more striking when one examines the allied Eupagurids. The American *E. longicarpus* has chitin stretching into the anterior part of the abdomen, and in our own *E. prideauxii* it is found in about the fourth abdominal segment. In the present species the mid-gut does not cease till it joins the rectum in the fifth abdominal segment. At the base of the pyloric ampullae, at the origin of the mid-gut, the two ducts of the digestive gland originate, and immediately behind their point of origin, but on the dorsal surface, arise a pair of *pyloric caeca* (mid-gut caeca of Pearson). The caeca come off close together and run forward on the top of the stomach for a short distance, closely applied to its walls, and then dip down, passing slightly forwards, till they each end in an irregular coil underneath the stomach.

The **Digestive Gland** (or liver) may conveniently be described now. It consists essentially of a pair of axial tubules stretching from their origin under the stomach to a considerable distance into the abdomen, and giving off numerous diverticula (fig. 25). The axial ducts are round and broad in section, and during their passage through the thorax are applied closely to the latero-ventral side of the alimentary canal. The caecal diverticula which arise from this part are few and short, but when the central ducts have passed the peduncle, they separate from the gut and run the remainder of their course on the surface of the flexor muscles of the abdomen. It is from

this part of the tubes that the bulky mass of branching diverticula which fill the cavity of the abdomen arises. The gonads are usually imbedded in the liver, and the alimentary canal either passes between the two lobes or through the right portion. The tubules are not packed very closely together, and they therefore retain in section their circular outline. The digestive gland is copiously supplied with blood by the superior abdominal artery and its branches.

The course of the mid-gut is uninterrupted till it joins the rectum. It is a thin-walled smooth tube, without convolutions, through which the faecal matter can be seen. Just before the rectum a long unpaired caecum (*caec.*, fig. 25) arises from its dorsal surface, which passes backwards between the liver tubules to the dorsal surface of the mass, and terminates in a small coil in the third abdominal segment—a little beyond the testis in the male. The caecum seems to be usually longer in the male than in the female. It has been very badly named the "*hind-gut caecum*," seeing that it arises from the achitinous part of the alimentary canal. There is apparently considerable variation in the place of origin of this unpaired caecum among the Eupagurids, though it is always derived from the mid-gut. It appears to form some index to the extent of the chitinous lining of the hind-gut, as it always comes off at the junction of the two parts. M. T. Thompson describes it in *E. longicarpus* as passing from the thorax back into the abdomen—the reverse direction of *E. bernhardus*—and in *E. prideauxii* it arises in the fourth abdominal segment more than half-way up the abdomen, and is comparatively short.

Hind-gut.

The **Rectum** is from two to three centimetres long in a full-grown animal. It is thick-walled and muscular, and packed with the rosette-shaped glands mentioned above. The walls are considerably folded internally and have a thick chitinous lining. They are richly supplied with blood from the plexus of vessels which covers them.

The **Anus** opens on the under surface of the telson and is surrounded by a sphincter muscle. In the living animal the rectum exhibits vigorous peristaltic movement.

Histology of Alimentary Canal.

The walls of the oesophagus are formed of very long narrow cells, with a thick base of fibrous connective tissue and an outer layer of muscle fibres. The lumen is lined with cuticle. Mention has already been made of the glands on the oesophageal walls. The cuticular lining is continued through the stomach, and the gastric mill is formed by calcifications in its substance. No other histological feature of the stomach calls for notice.

The lining of the mid-gut is very characteristic. The cells are columnar, with large nuclei and considerable contents of fatty matter. They have a striated border which appears in sections as a dark lining to the cells. The muscle layers at the base are frequently thrown into small plications.

The epithelium of the hind-gut (fig. 22) is more regular than that of the achitinous gut. The nuclei are smaller and there are very scanty cell contents. A thick chitinous layer lines the gut. Behind the basement membrane is a wide layer of muscle bundles and glands which are arranged in very definite clumps. A layer of connective tissue with blood vessels and nerves surrounds the whole. The structure of the paired and abdominal

caeca gives no clue to their function. The cells are long and columnar, with small oval nuclei situated near their base. They have a striated border similar to but narrower than that of the mid-gut. The cavity is occluded by the much folded walls.

The histology of the digestive gland differs somewhat from that described by Pearson in Cancer. The so-called "fat cells" are never scattered round the lumen, but bulge out from one point only at a time (fig. 23). It seems doubtful whether the division into "fat" and "ferment" cells can be justified, and whether the fat cells are not to be considered only as ferment cells engaged in excretion. These cells have a very distinctly striated border (fig. 24). Small deeply-staining cells are found between the larger ones. They probably give rise to the ferment cells. The nuclei of the "ferment" cells are to be found two-thirds of the way from the periphery, those of the "fat" cells at their extreme base, nearly all the cell being filled by the huge oil globule.

BLOOD VASCULAR SYSTEM (Pls. III and IV).

With the exception of the portion of the blood system which relates to the abdomen, the course of the blood, both arterial and venous, is that of a normal Decapod Crustacean. As in the crayfish or the crab, the pure blood from the gills passes to the pericardium and is driven by the heart through definite blood-channels to the various parts of the body, whence it returns for aeration by means of irregular sinuses to the gills.

The **Heart** (fig. 28) lies in a space, the pericardium, situated directly under the cardiac part of the carapace. It appears pentagonal in shape from above and rectangular from the side, though not so markedly

as in the case of the Macruran and Brachyuran heart owing to the extension of the postero-inferior angle. Viewed from behind, it has a distinct sinistral inclination. The walls are thick and strongly muscular, and the cavity in older specimens is almost filled by the strands of muscle which pass across it. The blood enters the heart by three pairs of ostia provided with flaps opening inwards—one pair placed antero-dorsally, one latero-ventrally, and one postero-laterally. Seven vessels leave the heart, three passing forwards, three downwards, and one backwards.

The heart-beats are regular in any one individual, but there is some variation in different specimens. The contractions are very explosive, and each contraction draws in the anterior end of the heart, stretching the two lateral and median arteries at the same time.

The **Pericardium,** whose walls have the same general outline as the organ they enclose, is a fairly spacious thin-walled cavity extending from the cervical groove anteriorly to the beginning of the eighth thoracic somite posteriorly. It rests ventrally on the mid-gut, and dorsally is applied closely to the carapace. On either side of the posterior part of the pericardium there is a shallow cavity. These possibly represent the "poches pericardiales" of Brachyura. The blood is brought to the pericardium from the gills, and passes through the ostia to the heart.

The various spaces in the body which are filled with blood do not represent a true coelom. They are morphologically a part of the vascular system which has become greatly distended and which has been termed by Lankester a haemocoel.

A portion of the renal organ and the gonadial sacs may possibly represent the true coelom of other animals.

The **Arteries*** (figs. 25, 26 and 27) leaving the heart are for the most part easy to trace, but the dissection is greatly facilitated if about a cubic centimetre of strong borax-carmine or methyl-green solution in water be introduced into the heart of the living animal by a hypodermic syringe an hour before it is killed. It is advisable to stupefy it with a weak solution of alcohol before operating, and the hole in the carapace can be conveniently stopped by a drop of hot wax. The stain will be found to have attached itself to some extent to the walls of the vessels, which are thus rendered visible throughout their courses. Three main trunks run forwards from the heart, the median cephalic (or ophthalmic) artery, and the paired lateral (or antennary) arteries (fig. 25, Pl. II).

The *Ophthalmic* artery (*opth. a.*, fig. 25) lies close to the surface; it may be seen through the carapace in injected specimens. Passing over the top of the stomach without giving off any important branches, it plunges down and divides into two vessels, one on either side of the brain, which supply the region of the front of the cephalon. The vessel is dilated into a flask-shaped bulb just in front of the heart.

The *Lateral* arteries (*ant. a.*) arise on either side of the cephalic artery. While the median vessel rises on leaving the heart in order to surmount the stomach, the lateral arteries turn sharply outwards and pursuing a level course on either side supply both that organ and the surrounding tissues with branches. At their anterior extremities the arteries bifurcate and give numerous branches to the excretory organ and muscles which lie laterally in the cephalon.

* For a comparative study of Decapod arterial systems see :—
Bouvier, *Ann. des sci. nat., zool.*, Ser. 7, Vol. XI, 1891, p. 197.

The *Hepatic* arteries (*hep. a.*) are given off from the sides of the heart. They are small and have no longer the important function which is assigned to them in the Macrura and Brachyura, and their part in supplying blood to the liver has been entirely taken over by the superior abdominal vessel. They terminate in small twigs on the gut.

The *Sternal* artery (*d. st. a.* and *st. a.*, figs. 26 and 28) is the largest and most prominent vessel connected with the blood supply. It arises in the median line at the extreme postero-ventral corner of the heart just underneath the superior abdominal vessel, but while the latter follows in the thorax the course of the gut, the former immediately swings to the left and plunges downwards. After passing the intestine, the sternal artery turns forward sharply and runs horizontally from the seventh to the fifth thoracic somites, when it again turns down and pierces the central ganglionic mass between the nerves of the second and third pairs of pereiopods. Under the nerve chain the vessel divides into anterior and posterior branches, running towards the head and tail respectively (fig. 26). This portion of the vessel may be conveniently called the inferior thoracic portion of the sternal artery. The anterior portion of this ventral artery gives branches to the chelae and the mouth parts, and two median branches ascend through the central ganglionic mass to supply the lower part of the stomach, the caeca, and part of the renal organ. After the branches to the first maxillipedes have been given off, the vessel divides, the two branches pass to the front of the oesophagus and anastomose on its walls, without, however, forming a ring. From each side branches to the maxillae and mandibles arise.

The posterior portion of the sternal artery is typical

up to a point, in that it gives segmental branches to the remaining thoracic limbs, but in the adult, and in all probability in the larva, it never passes into the abdomen. This artery, in fact, divides in the sixth thoracic somite into right and left branches, which supply the last pair of pereiopods. Small ascending arteries are given off with all the branches to the pereiopods.

The blood supply to the abdomen is entirely carried by the *Superior Abdominal* artery (*s. abd.*), and the vessel has undergone remarkable adaptation for its extra duties. A large trunk leaves the heart just above the sternal artery and passes above the gut—only giving off small branches—as far as the first abdominal segment. Here it divides into two large vessels. One (*seg. a.*) passes directly downwards to the right, turns backwards, and runs on the top of the flexor muscles. It divides in the third segment into sub-muscular and supra-muscular branches. The former follows the course of the nerve cord and terminates near the last ganglion; the latter gives numerous branches to the liver and gonads and finally divides into branches supplying the uropods, telson and rectum. The other vessel (*s. abd.*), veering slightly to the left, continues on the surface of the liver and supplies the gonads and pleopods. In the female we have the interesting condition that each ovary is partly supplied by one vessel and partly by the other (fig. 27); in the male the morphological left testis is supplied by the ventral (right) branch, while the right testis is supplied by the dorsal (left) branch.

M. T. Thompson finds in the young animal that the fourth zoea and the glaucothoë stages have a superior abdominal vessel with segmental branches, but that on the metamorphosis into the adult all these branches are

lost except part of the right one in the second segment. A new artery arises from this branch; it assumes the function of an inferior vessel and develops into the prominent ventral division of the superior abdominal artery present in the adult.

This modification may have been due primarily to the animal's assumption of a shell, and secondarily to the fact that nearly all the organs of the body—which in other Decapod Crustacea are supplied by separate thoracic arteries—are to be found in their bulk extended into the abdomen. One may conjecture, in the first place, that the pressure of the shell on the under-surface of the body would constrict a ventral vessel, especially at the peduncle, in such a way as to make its output of blood inefficient. In the second place, a vessel so remotely connected with the heart as the inferior abdominal, under these disadvantageous conditions, would be of little value in maintaining an efficient flow of blood through the large number of slender ramifying vessels required by the abdominal organs. Its place would tend to be filled by one more directly in communication with the means of maintaining the circulation. Thus the superior abdominal artery, whose size and proximity to the heart qualify it for the task of providing a large quantity of blood, has come to monopolise the supply to the abdomen.

Blood Sinuses and Veins.—The whole of the space inside the body walls might be theoretically considered as one large sinus containing impure blood. The presence of the viscera divide this space up into several smaller sinuses, which are, however, all connected with each other.

Above and in front of the stomach there is a distinct blood space—the *Dorsal sinus.* The main sinus with

which the outer afferent vessels of the gill lamellae communicate runs ventrally the length of the thorax. This *Sternal sinus* is continuous with the cavity of the abdomen, which constitutes one great *Abdominal sinus*. The sternal sinus does not communicate directly with the gills, but is connected to the *Infra-branchial sinuses* on each side of the body, into which the gill vessels open—by five distinct clefts on either side—the *Branchial sinuses*. Into the infra-branchial sinuses also open the haemal cavities from the thoracic limbs.

The *Afferent Branchial veins*, mentioned above, run from the infra-branchial sinus up the outer side of each gill. The blood is conducted down the inner side of the gill lamellae by the *Efferent Branchial veins* to the five *Branchio-cardiac veins*, which open by three slits on each side into the pericardium.

The **Blood** is a slightly opalescent but almost transparent fluid in which corpuscles float. The presence of haemocyanin gives it a faint bluish colour, which becomes intensified if the blood be left exposed to air. It coagulates under such conditions to a grey-white solid. The setting is effected by clear amoeboid cells which float in the lymph. Several kinds of cells (or amoebocytes) are to be found in the blood, but, according to Cuénot,* they constitute a series of stages in the breaking down of one kind only. The principal amoebocytes are semi-transparent amoeboid cells with large nuclei and finely granular cytoplasm. These cells increase in size and become full of eosinophilous granules. The almost solid body of granules is a prominent object in the blood at this stage, and amoebocytes in this condition are known as eosinophilous amoebocytes. The

* *Archives de Biologie*, T. XIII, 1895, p. 245.

cell now degenerates and it is eaten by the clear amoebocytes, which exercise a phagocytic function until the granules make their appearance in them. The granules from the degenerating cells appear to be dissolved by the lymph.

RESPIRATORY SYSTEM.

The branchial cavity is a part of the external world bounded on the inner side by the epimera, and above and on the outer side by a lateral flap of the carapace, which is called the branchiostegite. The gills lie on the epimera. The inflected portion of the carapace is in other higher Crustacea strongly calcified, but in the Pagurids it is always membranous and thin. Consequently the gills are far more exposed than is usually the case. Certain calcified bars serve as some support for this membranous flap, which is quite free, so that water can enter the branchial chamber from all sides except the roof. The action of the scaphognathite keeps the water in circulation over the gills.

The branchiae are phyllo-branchiate—that is to say, composed of numerous flat lamellae placed transversely to a central axis. On the inner side of each axis runs the efferent branchial vessel, and on its outer side the afferent branchial vessel. The gills are smaller in front than behind, and they are all pyramidal with their apices pointing upwards.

All the gills are arthrobranchs but one on the twelfth segment, which is a pleurobranch. No podobranchs are present.

The gill formula is the same on both sides, viz. :—

Segments	vi.	vii.	wiii.	ix.	x.	xi.	xii.	xiii.
Arthrobranchs	0	0	2	2	2	2	2	2
Pleurobranchs	0	0	0	0	0	0	1	0

In minute structure the gills are seen to be covered by a thin sheath of chitin, beneath which is a single layer of cells, the epidermis. The lamellae consist merely of this epidermal layer with its chitinous investment on both sides, separated by irregular spaces. A distinct vessel—the outer lamellar sinus—runs round the outer edge of each lamella. It is in communication with the cavity of the lamella (the lamellar sinus). The central axis is dumbbell-shaped and besides connective tissue there are two other kinds of cellular structures to be found in it. These are the branchial excretory cells and the branchial glands first described by Allen in *Palaemonetes.** There are two kinds of these latter structures, and Allen's observation as to their different positions in the animal he studied holds good for *E. bernhardus*. The reticulate glands are distinguished by the fact that the cytoplasm of their cells appears as a deeply staining network, the nuclei are spherical and lie near the base, and the ducts and the nuclei belonging to them are very distinct. The protoplasm at the apex of each cell stains deeper with Erlich's haematoxylin and säurefuchsin than the remainder. This type of gland is almost exclusively found round the efferent vessels. The other type of gland is characterised by the absence of the network, the smaller size of the individual cells and the larger relative size and more central position of the nuclei. It is also much more difficult to follow their ducts and distinguish the nucleus of the duct. This type of gland stains very lightly, and is neither so abundant nor so prominent as the reticulate type. It is generally found round the afferent vessels of the gill axis. In general structure these branchial glands are precisely similar to the stellate cells which are present in the

* *Quart. Journ. M.S.*, Vol. XXXIV., p. 75, 1893.

alimentary canal, in the dermal layer of the body wall, and on the under side of the abdomen. Cuénot states that the branchial glands give a mucoid secretion.*

EXCRETORY SYSTEM (Pl. IV).

The Renal excretory system of the Hermit Crabs has attained a complexity which no other Crustacean exhibits. In addition to the complex arborisations which ramify between the viscera in the cephalo-thorax, there is (in the present species) a large unpaired abdominal sac. All this belongs to the antennary gland ("green gland") system.

Excretion is also performed by separate cells in various parts of the body—notably those in the gill axis, and an excretory function has been attributed to the "ferment" cells of the digestive gland.

It is not possible to make a dissection of the excretory system without previous treatment of the animal. A spirit specimen rarely shows more than the abdominal vesicle and the antennary gland, and, at best, indistinct traces of the remainder of the system; so it is essential to make a complete study on living material by means of injections.

The substances which are suitable, *par excellence,* for such injections are methyl-green and säurefuchsin in solution in sea-water. A fairly strong solution, the exact strength is immaterial, should be made of the pure substance. One or two c.c. may be introduced into the animal by means of a hypodermic syringe inserted in the arthrodial membrane under the thoracic limbs. The crab may now be returned to its shell and allowed to live for about forty-eight hours, after which it may be killed

* *Archives de Biologie.* T. XIII., p. 250, 1895.

and dissected. The antennary gland will not take the coloration, but the rest of the system will be distinctly outlined. It will be found that the colour has also appeared in the excretory cells of the gill axis.

In an injected specimen it will be found that there is an antennary gland situated in the front of the cephalon behind the second antenna, which communicates with a diffuse and complex spongy mass in the thorax leading to a thin-walled bladder, the nephrosac, in the abdomen, all of which represents the "bladder" of other Decapod Crustacea (fig. 29).

Except for the abdominal nephrosac and the median ventral thoracic mass, the system is paired.

1. The **Antennary Gland** (*g.g.*) consists of two parts, which communicate with each other, an inner—the end sac ("saccule") which is surrounded by an outer—the labyrinth. The whole is somewhat kidney-shaped and has a lobulated appearance. The connection with the bladder arises from the upper side, above the notch, and the artery supplying the gland passes in a little lower.

The end sac is slightly exposed on the dorsal surface of the antennary gland. Its cavity is broken by blood lacunae and by the extensive ramifications of its walls. Sections show that few prolongations arise from its dorsal side. The walls are irregular, and are often more than one cell thick. The cells are large and squamous, the nucleus is spherical and at the base of the cells, and the protoplasmic contents are light staining and finely granular. The borders of these cells are irregular and protuberant, and oil globules are often present (fig. 32).

The labyrinth is an intermediate duct between the bladder and the end sac, whose cavity has become excessively convoluted by ingrowths from its walls. The epithelium lining this portion is very distinct from that

belonging to the end sac. The cells are still squamous but much smaller, so the nuclei appear to be side by side in straight rows. The border of the cells is regular and without the lobed appearance which characterises that of the end sac. The cytoplasm is scanty and striated; it stains more strongly than that of the end sac. The labyrinth communicates by a narrow passage with the rest of the system.

2. The **Anterior Vesicular Mass** (Marchal)* comprises that portion of the system apart from the antennary gland, which lies in the thorax and cephalon.

The opening of the whole to the exterior is connected with this part of the system. The passage commences close to the connection with the antennary gland. It is at first wide, but rapidly becomes narrow, and passes downwards underneath the second antenna, where the external orifice is situated (fig. 30).

The arrangement of the Anterior Vesicular Mass is as follows:—The canal from each gland expands into a mass of ramifying tubules in front of the stomach (epigastric lobe). Although these two masses are close together in the mid-line, they do not communicate with one another. From each epigastric mass (*eg. l.*) a narrow branching canal runs backwards, closely applied to the muscles, to join another mass of arborescent tubules situated on either side of the stomach opposite to the depression between the cardiac and pyloric ossicle of the gastric mill. Branches from these two lateral paragastric masses (*pg. l.*) pass across the stomach in the above-mentioned depression to meet, but not to coalesce, in the mid-line (*sg. l.*).

Underneath the stomach is a median unpaired

* *Archiv. de zool. expérim. et gén.*, Ser. 2, Vol. X, 1892, p. 57.

portion (*m. v. l.*), which is connected by anterior and posterior branches to the two lateral masses. The remainder of the system comes under Marchal's head :—

3. The **Posterior Vesicular Mass,** which includes the unpaired bladder in the abdomen and its connecting tubes with the two paragastric masses.

The connecting tubes are a pair of branching ducts which run on the top of the alimentary canal side by side till they reach the abdomen, when they unite in a large thin-walled vesicle (*bl.*) of considerable extent—rather the shape of a centrifuge tube—which is about three-quarters the length of the abdomen. It is called the nephrosac. The walls are composed of squamous epithelium with striated cytoplasm at its base and a large spherical nucleus in the centre of each cell (fig. 31). There is a distinct dark border to the cells of the labyrinth and vesicular masses, which is probably due to a striated margin or "Härchensaum." The bladder is tucked between the lobes of the digestive gland—or between the ovaries in the female.

As the excretory system lies wholly in the venous blood sinuses of the body, excretion is probably carried on by direct diffusion through the walls. In sections of the vesicular masses cells may be seen with their inner portions projecting as a clear vesicle into the cavity of the organ. These vacuoles may be shed as small bladders into the lumen, or the entire cells in the end sac are nipped off and pass to the exterior. The excretory fluid is full of such bladders and single cells.

NERVOUS SYSTEM* (Pls. IV and V).

The nervous system of Eupagurus shows little trace of the asymmetry which involves so many other parts of the animal. The variations in position and size which occur in the nerves supplying the opposite sides of the cephalo-thorax are exhibited in any higher Crustacean, but the twist of the abdomen necessarily causes a certain amount of alteration of the abdominal portion of the nerve-cord. There would be no reason to expect any further modification in a system which is not of large bulk, and whose functions are in no way altered by the change in symmetry.

The degree of concentration of the thoracic ganglia is intermediate between that of the Macrura on the one hand, and of the Brachyura on the other. They are not disposed in a diffuse chain as are those of the Crayfish, nor are they indistinguishably fused as in the common Crab, but the concentration is carried to a stage in which the individuality of the ganglia has been lost, while a more general division into regions representing the fusion of two or more ganglia is preserved. Thus the central thoracic ganglion-mass can be differentiated into three (or perhaps four) main portions, which respectively supply the mouth parts and chelae, the first pair of walking legs, the second and third pairs of legs, and the fourth pair.

The nervous system may be conveniently described in three portions: the brain and its connectives, the thoracic ganglion-mass, and the abdominal chain.

The **Brain** or supra-oesophageal ganglion (fig. 37) is situated in the mid-line, under the anterior margin of the cephalo-thoracic shield, behind the eye-stalks and

* For a comparative study of Decapod nervous systems see :— Bouvier, *Ann. des sci. nat., zool.*, Series 7, Vol. VII, 1889, p. 73.

above the epistoma. It is transversely ovate from above, and a bi-lobed appearance is given to it by a shallow median depression.

The nerves supplying the principal sense organs and the circum-oesophageal connectives with their offshoots arise from the brain, and branches are also given to the surrounding tissues.

Optic nerves (*n. op.*).—A pair of nerves arise in the front of the brain and pass, diverging slightly, into the eye-stalks. Immediately after passing the base of the peduncle the nerve swells to form a small ganglion, from which fibres supplying the eye muscles arise, and ends in another enlargement under the retina.

Oculo-motor nerve (*n. m. o.*).—The muscles of each eye and its adjacent parts are innervated by a much smaller nerve, which pursues a track parallel to and outside of each optic nerve.

The *Antennulary nerves* ($n. a._1$) are really four in number, but owing to the fact that the nerve supplying the first antenna and that supplying the otocyst have coalesced on either side, a single pair only is visible. This pair arises from the under surface of the posterior half of the brain. Each nerve is broad and has but a short course, plunging downwards and forwards on leaving the brain into the peduncle of the limb, where it divides into auditory and tactile and muscular branches.

The *Tegumentary nerves* (*n. teg.*) arise on either side of the brain, slightly above and behind those supplying the first Antenna. Each nerve is broad and prominent, and passes outwards and slightly forwards, surrounded by the mass of excretory gland which envelops the hinder part of the brain. It branches frequently and supplies the integument and other tissues in the front of the head.

A pair of *Antennary nerves* (*n. a.*$_2$) originate behind the Tegumentary nerves. These long and slender nerves pass outwards at right angles to the long axis of the body till they turn sharply forwards towards the second Antennae.

The Brain is connected to the remainder of the nervous system by a pair of long connectives—the *Oesophageal Commissures* (*cm.*)—which arise close together at the back of the brain and curve gently outwards round the oesophagus, to approximate again as they approach the thoracic ganglion-mass. On either side of the oesophagus each commissure dilates to form a par-oesophageal ganglion, from which arise four nerves. Both of the two outside branches are small; the anterior one, which is the smaller, innervates the surrounding tissues, and the larger and posterior one supplies the muscles of the mandible.

Stomatogastric system (figs. 39 and 37).—The two inside branches arise together and pass, diverging towards the mid-line in front of the oesophagus where each joins its fellow from the opposite side, to merge into a median unpaired nerve passing vertically up the front of the stomach. Three-quarters of the way up the anterior wall this median stomatogastric nerve enlarges to form the stomatogastric ganglion, from which several small branches to the muscles and walls of the stomach arise. The stomatogastric nerve then mounts the stomach and, directly on attaining its dorsal surface, forms another ganglion, which gives origin to several small nerves, and finally terminates in a bifurcation above the pyloric portion of the stomach.

After leaving the par-oesophageal ganglia, the commissures pass backwards and become attached close together to the front of the ventral thoracic ganglion-

mass. A slender transverse nerve—the post-oesophageal connective—joins the two commissures a short distance behind the oesophagus.

The **Thoracic Ganglion-mass** (fig. 37), in which the oesophageal connectives terminate, lies over the sternal artery on the endosternal plates of the third to sixth thoracic somites. Inward projecting processes from the dorsal parts of the endosternites partly bridge over the valley in which it is found. It is composed of three large masses of fused ganglia, which are divided from each other by constrictions; the first and second of these are somewhat rectangular in shape, and the third is pyriform. A shallow semi-circular groove on the third division marks the separation of the ganglia which are the centres for the fourth and fifth pereiopods from those which belong to the first abdominal segment.

The Central Thoracic Nerve-mass is pierced in the mid-line in three places for the passage of arteries. The most posterior of the three is a huge foramen, through which the descending portion of the sternal artery passes; the others are small perforations which are almost indistinguishable in any but specimens injected for the blood system (*asc. a.*).

Seven paired ganglia take part in the formation of the anterior mass, and seven nerves radiate outwards from it on either side. Those supplying the mouth parts usually come off separately, but there is considerable variation in their arrangement. The branches from the first and second Maxillipedes often coalesce before joining the main nerve trunk, and, less frequently, fusion takes place between the nerves supplying the pairs of Maxillae. The thoracic ganglion mass is symmetrical throughout, so only one side need be described.

The First nerve originates close to the oesophageal

commissure and is sometimes bound up with it for a short distance. It is quite slender—the seven nerves increase in size in proportion as we go backwards—and passes directly forward to the mandible.

The Second and Third nerves pass directly to the maxillae, and the Fourth, Fifth and Sixth to the maxillipedes.

The Seventh nerve, which is very broad, comes off at the widest part of the anterior lobe and passes slightly forwards to the chela. With this and the succeeding thoracic nerves two small branches arise which pass upwards and innervate the neighbouring tissues.

The central lobe of the thoracic ganglion-mass is the product of the fusion of but a single pair of ganglia, whose nerves supply the second pereiopod. The remainder of the thoracic limbs are innervated by branches arising from the posterior lobe. They all pass backwards and then turn sharply outwards, as they reach the segment for which they are bound. The thoracic nerve mass shades into the abdominal commissures, which—at first bound together—separate themselves as they enter the abdomen.

The **Abdominal Nerve Chain** (fig. 38) is of the familiar ladder type. There are five paired ganglia. Each pair, however, is almost indistinguishably fused, and they are connected by paired commissures. The five paired ganglia are situated in segments two to six, that belonging to the first segment being fused with the thoracic ganglion mass. From each ganglion branches are given off in a somewhat irregular fashion to the muscles, integument, and to the pleopods, and at least one pair of nerves arises from the inter-ganglionic commissures.

The nerve chain lies under the bulky flexor muscles and over a thin layer of integumentary muscles.

On entering the abdomen the chain slews to the left, passing through the "columellar" muscle to the first ganglion (second abdominal ganglion) in the second segment. This is placed well on the left side of the body, and in a lesser degree so is the third segmental ganglion, which is close to the second, and the fourth. From the fourth to the fifth ganglion there is a longer stretch of connective, which once more brings the chain into the mid-line of the body; and there is another long pair of connectives passing from the fifth through the flexor muscles, till they join the sixth ganglion on the dorsal surface of the muscles under the posterior end of the rectum. From this ganglion branches are given to the uropods, the telson and the alimentary canal. There is a ring round the rectum, but it is uncertain whether there is any actual junction between the two nerves.

The histology of the nervous system in the higher Crustacea is a rather difficult specialised study, which the ordinary student of Zoology will probably not attempt. More advanced workers should refer to the detailed account of the histology of the shore crab (Carcinus), given by Bethe in the following papers:—

Arch. f. mikroscop. anat., v. 44, 1895, p. 579.
Ibid. ... ... v. 50, 1897, p. 460.

SENSE ORGANS (Pl. IV).

The sense organs consist of a pair of compound stalked eyes, a pair of otocysts, and a number of sensory setae scattered over the body.

The Eye* (Figs. 33 and 34).

The optic peduncle, at the end of which the eye is situated, is a two-jointed structure. The basal joint is short and thick, and it bears on its inner side a spearhead shaped "squame"; the distal joint is long and cylindrical, but narrower in the middle than at either end. The two parts are loosely joined by membrane and the outer moves freely on the inner. The cornea takes up all the anterior end of the second joint. It is circular in outline except for a small invasion of the calcified portion of the stalk on its dorsal and inner side.

The eye is compound—that is to say, it is composed of many separate, similar parts or elements, each of which is called an ommatidium.

The cornea is facetted, and each such area is hexagonal in shape. A fine line bisects each facet diagonally from angle to angle. These corneal facets are the outer ends of the ommatidia, which, owing to the convexity of the cornea, converge inwards radially.

An ommatidium (fig. 33) is a definite arrangement of five kinds of cells in a cluster about a central axis. The cells comprising each ommatidium may be enumerated as follows:—(1) Corneal hypodermis (secretes the facet of the cornea immediately above it); (2) Cone cells; (3) Distal retinular cells (Iris cells, Hesse); these three kinds constitute the dioptric portion of the eye; (4) Proximal retinular cells, which, together with the rhabdome, constitute the receptive portion of the eye; (5) Accessory cells (Tapetum cells, Hesse).

(1) According to G. H. Parker there are two *corneal cells* (*c. hy.*), and the fine line bisecting the facet of the cornea is the line of their division, but Schneider states

* See also Note, on p. 73.

that they are four in number. These cells are squamous and tile-like, but their boundaries are very indistinct.

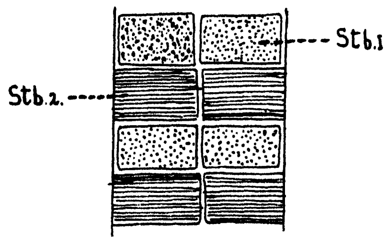
(2) The *crystalline cone* (*vit.*) is composed of four cells, and it extends from the corneal cells to the distal end of the rhabdome. Each cone cell has a transparent body tapering to its proximal end, which overlaps the distal end of the rhabdome. The nuclei are at the distal end of the cells.

(3) There are two *distal retinular cells* (*d. re.*) at opposite sides of the cone cells. They are deeply pigmented and are contractile, their size varying with the strength of light.

(4) There are seven *proximal retinular cells* (*p. re.*), and Parker has found that there is typically an eighth which has become rudimentary. These cells surround the rhabdome. Their distal ends—by the side of the cones—are bulbous and contain the large nucleus, the proximal end tapers off above the basement membrane. The optic nerve fibrillae pass through the cells to end in all probability in the "stiftchen" of the rhabdome (fig. 33). They run up the outside of each retinular cell, pass round the nucleus and return down the inner side. It is this bundle of fibrillae round the nucleus which gives the bulbous appearance to the distal end of the cells.

The retinular cells are deeply pigmented from end to end and thus form a complete dark sheath round the rhabdome. Parker found that in the darkness the pigment migrated completely into the retinal fibres beneath the basement membrane, so that the rhabdome became accessible to light from all sides. Similar changes are induced by darkness in the distal retinular cells (Iris cells), the pigment all retreating into the body of the cell at its distal end. In daylight the pigment extends down the proximal processes of the cells.

The *rhabdome* is a complicated structure, narrow and spindle-shaped (figs. 33 and 34 and Text-fig. 2), which used to be described as consisting of four parts, a fact which induced Grenacher to conclude that it was secreted by alternate retinular cells. It is now known that the quadripartite appearance and form is illusory, and is due to the peculiar manner in which the retinular cells form the structure.



TEXT-FIG. 2.

Every two retinular cells (reckoning the seventh one as double) take part in the secretion of one quarter of the rhabdome. These quarters—which may be separated and are known as rhabdomeres—are each made up of transverse plates alternately supplied by the two cells (fig. 34). Any one retinular cell would have a toothed or cogged appearance if it were separated with its own portion of the rhabdome. The whole rhabdome therefore is built up of a series of transverse half-plates and Text-fig. 2 would represent a diagrammatic eccentric longitudinal section in which the "stiftchen" of each lamella are shown alternately with cut ends and from the side. The arrangement reminds one of the dovetailing of the edges of a box. In transverse section the rhabdome is almost square, and it is surrounded by a distinct investing sheath ("Schluss-leisten," Schneider). Each of the half plates bears a

border of "stiftchen," and it is probable, though not certain, that the nerve fibrillae, passing through the retinular cells from the optic nerve, communicate with them. At the distal end of the rhabdome is a pear-shaped cavity, first described by Parker, filled with a coagulable fluid (fig. 33).

(5) Irregular cells, lightly pigmented, are found at the base of the rhabdome and on both sides of the basement membrane. Parker, who calls them *accessory cells*, thinks they are probably mesodermic. The nerves from the ommatidia pass into a mass of nervous tissue, underneath the retina, which contains four successive ganglia, and thence to the brain.*

Various observers have given conflicting accounts of the type of image which is thrown on the retina of the Arthropod eye. From the most recent researches, however, there is little doubt that the image in the compound eye is a single upright one for the whole retina, whose perceptive elements, the rhabdomes, receive each a single impression. Parker has succeeded in obtaining all the results of previous observers by preparing the eye in different ways, and by pointing out where they failed has practically proved that each ommatidium does not receive a small complete image.

The Otocyst (figs. 35 and 36).

The otocyst or auditory sac is situated in the proximal joint of the first antenna. There is a small bulbous prominence on the outside of the joint in which it lies, and it opens to the exterior by a narrow

* The classic paper on the Arthropod eye is by Parker in the *Bull. Mus. Comp. Anat.*, Harvard, Vol. XXI, p. 45. In details of finer histological work it has been superseded by Parker's further paper in *Mitt. a.d. Zool. Stat. z. Neapel.*, T. XII., 1897, and by Hesse's in *Zeit. Wiss. Zool. Wien.*, Bd. LXX., p. 347.

longitudinal slit on the dorsal surface, two-thirds up the joint from the posterior end. The opening is guarded by two fringes of setae, an upper fringe of simple styliform hairs springing from the inner edge and passing diagonally forwards across the opening, and a lower fringe of large, somewhat fusiform, densely plumose hairs springing from the outer edge of the opening, and directed at right angles to the upper fringe.

The otocyst itself is attached by its anterior end, underneath the opening to the exterior, and extends backwards for about one-half the length of the entire joint. It is a simple gourd-shaped sac with chitinous unfolded walls, which are often—with the exception of a small portion of the dorsal surface—lightly calcified. The stalk of the gourd is at the extreme posterior end of the sac, and is turned towards the mid-line, so the sac appears to lie on its side. This small caecum has been unfortunately named the "cochlea," in reference to an imaginary resemblance to that structure of the vertebrate ear. The interior of the "cochlea" is always minutely spinose. A slight carina runs from the "cochlea" round the outer side of the sac, and a shallow groove from the same point along the ventral side contains the otic branch of the antennulary nerve.

The interior of the sac is not complicated by any irregularities, but follows precisely the lines of the outside. The sensory region is to be found on the floor, and the special "auditory" setae are roughly arranged in two or three rows diverging from the "cochlea"; the greater number of setae spring from the slight ridge of the otic nerve on the outer side of the sac, while the remainder are placed in an irregular row on the inner side supplied by a smaller nerve branch. They are of one kind only—small, straight and plumose, miniatures

in all but the base, of the fringing setae already described (fig. 36). Each hair is a hollow tube attached by a membranous base to a knob-shaped podium, in which the single nerve fibre supplying the structure terminates. Thus the hair is only capable of extensive lateral movement at the membranous base in direct contact with the nerve element.

Many sand particles, of all sizes small enough to enter by the orifice, are found free in the lumen of the sac or adhering to the setae. The nerve supplying the sensory region impinges on the sac at its posterior end on the ventral surface, and at once divides into a more ventral broad portion which curves nearly round the outer side of the sac, and a smaller branch passing to the inner side.* It is unnecessary to deal with the functions of the sac in detail. Prentiss† gives an exhaustive account of the work of earlier observers and supplements it with his own experiments. A feeling for the picturesque in the earlier naturalists, aided by inconclusive experimental work, led them to assign a sense of hearing to Crustaceans only differing in degree from our own; but, after a period in which both opinions were held, the general view now is that the otocysts are almost exclusively static in function, and are only concerned in the orientation of the animal.

Olfactory and Tactile Setae.

Other sensory setae of a simple kind are found in most parts of the body. They consist of a hollow shaft, which communicates with a single nerve fibre. On the

* An inaccurate account of the otocyst of this species (under the name *P. streblonyx*) by Farre, may be found in *Phil. Trans. Lon.* 1843.

† *Bull. Mus. Compar. Zoöl.*, Harvard, Vol. XXXVI., No. 7, p. 168, 1901.

first antenna another type of setae is found. They are in a dense bunch on the upper side of the exopodite and are known as olfactory setae. Each seta is a long, tapering, flattened shaft, with a large number of joints—about two dozen—placed on a wide base. It is hollow and appears to open by a minute pore at its distal end. Round each basal joint is a small bunch of minute hairs. The exopodite is a strongly annulated conical structure, and each ring bears several of these long setae. In life the crab continually flicks its antennules, spreading the setae at each flick. Each seta is supplied with a large number of nerve fibres.

MUSCULAR SYSTEM.

It is unnecessary, for the purposes of this Memoir, to enter into a full description of the muscular system of the Hermit Crab. A detailed account of the muscles of a fairly typical Decapod Crustacean has been given in the Memoir on Cancer*; and though the present type has closer affinities with the Macrura than with the Brachyura, so far as the present system is concerned, no useful purpose will be served by enumerating muscles which have their counterpart throughout the Order. Certain parts, however, of the muscular system have undergone profound modification due to the mode of life of the animal, and of these parts an account, based entirely on M. T. Thompson's† work on the metamorphosis, will now be given.

It is the musculature of the abdomen which diverges in the greatest degree from the normal. As practically all the movements of the abdomen are confined to flexion, the flexor muscles have become abnormally large

* Pearson, "Cancer" *L.M.B.C. Memoirs*, XVI.

† *Boston Soc. Nat. Hist.*, Vol. XXXI., No. 4, p. 147.

at the expense of the extensors. The muscles of the young animal in the early Glaucothoë stage only differ in detail from those of the Crayfish or Lobster. The extensors have a general longitudinal course and are well developed; the flexors comprise several muscles, the descending, transverse, longitudinalis and loop-enveloping, and pleopodal muscles independent of the flexors are present.

In the change to the adult crab the transverse muscles lose their fibres and disappear, and only remnants of the descending and lateral longitudinal muscles persist, so that the flexors come to consist of the ventral, longitudinal and the loop-enveloping muscles, the former of which are probably the more important. The pleopodal muscles also degenerate and the extensors are extremely weak. A thin layer of fibres—the integumentary muscles—lines the integument beneath the nerve cord; they are apparently derived from scattered fibres that lie in the same position during the Glaucothoë stage. The columellar prominence is derived from the ventral flexor muscles of the third segment. The flexors are bulky, and those of the right side are considerably larger than the flexors of the left.

There is nothing in the muscles of the cephalo-thorax which calls for comment.

REPRODUCTIVE ORGANS (Pl. V).

With the exception of the orifices of the sexual ducts, there is only one point in which the male *E. bernhardus* differs in external characters from the female. That difference is to be found in the abdominal appendages, so it is quite impossible to distinguish the sex of a Hermit Crab unless it be extracted from the

shell; but the right chela of the male is often more massive than that of the female. The male always shows much greater readiness to emerge from its shell than the female, especially if she be "berried." The pleopods of the female are four in number; they are on the left side only on segments two to five. The male has three pleopods, that of the second segment being absent, and they are all much smaller than the first three of the female. The fourth pleopod of the female is as much reduced as those of the male.

Male System.

The **Testes** (figs. 25 and 40) are paired and quite separate. They lie in or about the third segment of the abdomen, and the vasa deferentia open by a circular hole on the base of the last pair of pereiopods. Both organs are placed in the cleft between the two lobes of the digestive gland, the left on the dorsal side and the right against the muscles. Owing to the twist of the liver, the left testis has become topographically dextral to the right one. Both testes are flat, lozenge-shaped organs, and the superficial left one is slightly larger than the right, which is imbedded in the digestive gland in a laterally erect position. The vasa deferentia are large, prominent yellow tubes in the breeding season. They pursue a tortuous course till they reach the thorax, when they abruptly plunge downwards to the external opening.

Each testis is essentially a long and excessively convoluted tube, in the length of which the sperms may be seen in every stage from their origin as spermatoblasts to their final condition in their chitinous case. The greater part of the testis—the testis proper—is a narrow lobulated tube, which has become so intensely convoluted and involved that it has the appearance of a

solid mass. It is impossible to unravel this tangle, and the tube may or may not branch.

It is from the epithelium lining this portion of the testis that the gonadial elements arise. Some of the germinal epithelium cells enlarge greatly and are budded off into the lumen of the tube. These bodies have a large quantity of densely staining nuclear matter and scanty cytoplasm. They pass further down the tube, and each divides into many smaller bodies with large deeply-staining nuclei and again but little cytoplasm, and each of these in turn gives rise to a single spermatozoon. The former large bodies, which are more abundant in the higher reaches of the tube, are known as the *spermatocytes*; the smaller bodies formed by their division as the *spermatids*. A typical section through a testis follicle usually shows a large number of either spermatocytes or spermatids with spermatozoa (fig. 46). It is not often that both conditions are found in equal quantities in any one portion of the tube.

The spermatozoa continually pass down the germinal portion of the tube into a smooth, thick-walled area in which the chitinous cases for their reception are secreted. The epithelial cells lining this part are extremely long with oval nuclei situated at the end of their outer third. The cavity has become constricted and plum-stone shaped. The tube presently emerges from the tangle and is seen to be a continuation of the vas deferens. The portion in which the preliminary process of forming the spermatophores is carried on, lies in a very compact small coil on the surface of the general mass of the testis at its posterior end (*d. c.*, fig. 40), and in this coil the sperms are surrounded by a long smooth chitinous case, which is uninterruptedly continued until the tube begins to leave the above-

mentioned compact coil and pass forward as a more or less straight duct.

At the beginning of this straight portion signs of segmentation begin to appear on the upper side only of the chitinous tube containing the sperms (fig. 41). These constrictions deepen till the sperm band presents very much the appearance of the colon of higher mammals, and finally it becomes cut into a series of lobes united by a continuous base—each lobe containing a large number of spermatozoa (fig. 42). The lobes, as we go further down the tube, gradually assume the shape of the finished spermatophore (fig. 43), and on reaching the vas deferens, the strip of membrane on which they are placed like a fringe breaks into convenient lengths—four or five spermatophores being placed on each strip.

The vas deferens, which is crowded with such strips, is a thin-walled broad tube of considerable length. It becomes narrower on reaching the thorax and this narrow part is continued to the communication with the exterior—it is called the *ductus ejaculatorius*. The whole gonad from the germinal portion to the end of the ejaculatory duct is one uninterrupted tube.

Spermatozoa (fig. 44, *a* and *b*)—The sperms are quite characteristic bodies. They appear, in the living material, to consist of a clear capsule from which spring, near the base, three long processes. Stained preparations show that the detailed structure is based on the same lines as those usual among the marine decapod Crustacea. There is a vase-shaped head, down the centre of which runs a hollow column with dorsal and ventral orifices. The cephalic vesicle is clear and it rests on a collar from which three processes spring. Under the collar is a somewhat irregular vesicle of granular protoplasm, which readily stains. Retzius describes an anterior

explosion capsule and figures various stages in its development.*

FEMALE SYSTEM.

The **Ovaries,** like the testes, are situated in the abdomen, their ducts passing forwards into the thorax to open on the coxa of the third walking leg. They are also quite separate, and although the oviducts are very close to each other, they are never connected, a condition which seems to be uncommon but not unique in the Decapoda. In a mature specimen the ovaries take up a large part of the abdomen, both right and left gonads extending throughout its length. They are irregularly disposed, the left organ lying above its fellow at the anterior end, and, more posteriorly, on the right side of it.

Both organs are sausage-shaped bags of a deep purple colour in the living specimen. They present a granulated appearance when mature and the separate ova can be readily distinguished, but when spent they shrink to a fifth of their normal size, and are then a pale reddish colour. The oviducts are simply anterior prolongations of the ovaries. They arise without any very definite break and pass to the opening to the exterior without any convolution whatever. The internal structure of the ovary is not essentially different from that found in other Decapods.

The young eggs arise from a narrow band of epithelial tissue on the inner side of the ovary, extending its entire length. Although it is typically peripheral in position, in a mature ovary the crowding of the large eggs constricts its base and forces it to occupy a more

* Retzius. *Biolog. Untersuchungen*, Neue Folge, XIV.

nearly central position.* This band of tissue has been called by Ishikawa† the "germogen," to contrast it with the "vitellogen"—the rest of the ovary where the yolk elements are found. It is transparent in the fresh condition and is readily distinguishable from the purple eggs; in preserved material it is even more distinct, showing up white amidst the red ova. The ova in the ovary are enclosed in a follicular epithelium. The cells which are about to form the follicles are almost indistinguishable from the very young ova. The mature eggs are crowded together closely, and partly lose their rounded form by mutual pressure. The protoplasm of the ovarian egg has a characteristic radially striated appearance, and there is a membrane enclosing the egg—the primary egg membrane—which arises apparently from the peripheral protoplasm. A second membrane of a tougher nature, which is probably secreted by the cells of the oviduct, is present on the ripe egg. The walls of the oviduct before oviposition are very glandular. P. Mayer correctly states that there is but a single nucleolus in all the stages of the ovarian egg, and he also says that the freshly laid egg is not furnished with a nucleus and is a cytode. It is well known, however, that the chromatin of the germinal vesicle is often lost during maturation, and it is this phenomenon probably that accounts for the condition to which he refers.

The **"Cement" Glands** on the under-surface of the abdomen are accessories to the reproductive organs proper. They all consist of the type of gland we have noticed before—that is to say, a globular structure of pyramidal cells from the central cavity of which an

* Cf. Bumpus, American Lobster. *Journ. Morph.* V., p. 215, 1891.

† *Quart. Journ. M.S.* XXV., p. 391, 1885.

intracellular duct leads. The glands, which are profusely scattered on the under-surface of the abdomen in the dermis, secrete a mucous fluid which has been assumed to be the medium by which the eggs are attached to the pleopods. The exact method of attachment is still unknown, and nearly every observer of the egg-laying has a different theory of fixation. Huxley in his "Crayfish" considers that the eggs are coated with a viscid matter as they leave the oviducts* and Lereboullet, who has observed the process closely, is of the same opinion. The latter observer states that the cement glands are for the purpose of filling the "brood chamber" with mucus in which the eggs and sperms mix, and it is highly probable they have the same function in the Hermit Crab.

DEVELOPMENT (Pl. VI).

It is not known how fertilisation is effected in the present species. Copulatory organs are altogether absent, and neither the transference of the sperms nor the act of oviposition has ever been observed. Mayer (see below) argues from the apparent impenetrability of the outer coat of the egg when it leaves the oviduct that fertilisation must be internal. He is unable to offer any explanation of the method by which the free sperms gain access to the ovary. There seems no good reason why the egg coat should be considered to be more impervious to the sperms in Eupagurus than in the Lobster or Crayfish. In both of these animals fertilisation is undoubtedly external, and in the case of the Crayfish every step in the process has been observed. It is not possible for the Hermit Crab to form a brood pouch by flexing its

* Bumpus (loc. cit.) comes to the same conclusion with regard to the American Lobster.

abdomen in the same way as the Crayfish, without suffering some loss of the eggs, but the very fact that the cement glands are placed on the under-surface of the abdomen, instead of in their usual position on the pleopods, suggests that a similar process is gone through. Experiments on a female Hermit Crab will show that though glands on the pleopods would not be much use in filling a brood pouch formed by the flexion of the abdomen with secretion, similar organs on the under-surface of the abdomen would be very efficacious for that purpose. Fertilisation in such a chamber would be just as possible in Eupagurus as it is in the Crayfish. The empty spermatophores are almost always to be found adhering to the pleopodal eggs, and they can only have got there during oviposition. It is possible that the extended breeding season of this species is not unconnected with a certain wastage of eggs.

In brief, the process as conceived above would be as follows:—The male deposits the spermatophores on the under-surface of the female (possibly in a space between the columellar muscle and the body into which the oviducts open when the tail is flexed); the female flexes her abdomen underneath the thorax, fills the space with mucus, dangles her pleopods into the chamber and pours out the ova. The ova and sperm are mixed in the chamber, as in the Crayfish, and the eggs become attached to the pleopods, also as in that animal. The process of oviposition might possibly be carried on inside the whelk shell without flexing the abdomen.

Embryonic development.—The eggs are attached to the setae of the pleopods on the second, third and fourth abdominal somites in dense purple clusters.* Up to the

* The ova of *E. prideauxii* seem to be red, both ovarian and after extrusion.

eighth stage cleavage is total but somewhat abnormal, the nuclei dividing more rapidly than the blastomeres are formed, so that it is not before eight nuclei are present that segmentation occurs. The yolk is present in the cells as small fat bodies. The separation of yolk matter and protoplasm takes place on the egg dividing for the fourth time, and the nuclei becomes peripherally arranged, surface furrows indicating the boundaries of the cells. From this point segmentation is superficial. Gradually the centre of the egg breaks up and the protoplasm becomes confined to the single layer of cells on the outside, which encloses the yolk. It is unnecessary to follow the development further in detail, as it is quite normal from this stage.* A germinal disc appears, in the centre of which an invagination of the blastoderm forms a shallow gastrula. In front of the gastrula is the "anlage" of the abdominal region and further forwards the paired "anlagen" of the cephalon. The mesoderm proliferates from the cells in the front half of the gastrula and spreads forwards into the cephalic region. The gastrula cavity now closes and the hypoblast absorbs the yolk matter, pressing the epiblast to a thin surface layer. An invagination in front of the blastopore becomes the mouth and fore-gut, while the blastopore itself become the anus and hind-gut. The future mid-gut is formed as usual from the invaginated hypoblast.

Post-embryonic development.—The breeding season of Eupagurus is very extended, and at almost any time of the year females may be seen with eggs attached. The Zoeas are to be found in tow-nets from April to the end of September, and the Glaucothoë stage even later.

* Further details may be obtained from P. Mayer's paper in *Jen. Zeitschr. f. Naturw.*, Bd. XI., p. 188, 1877, from which the above account has been summarised.

The larvae are very delicate and difficult to rear in confinement, but one can get every stage in abundance in the plankton at Port Erin. The eggs remain on the pleopods until hatching time. The little Hermit Crab is now in the Protozoea stage, but the first ecdysis is accomplished as the larva quits the egg capsule, so the first free stage is in the form of a Zoea. To set the larvae free, the mother sits partly out of her shell and wipes the pleopods gently with the brush of setae on her last pereiopod to facilitate their escape. The same appendage serves to remove the husks from the pleopodal setae when the hatching is over.

A berried crab often exposes her eggs when her surroundings are peaceful, and fans them slowly up and down in the water by moving her pleopods. At an average the mother crab has about twelve to fifteen thousand eggs attached to her abdominal limbs at one time. Only a brief summary of the post-embryonic development can be given here; a detailed account of the American species *E. longicarpus*—which seems to agree in all particulars with ours—is given by M. T. Thompson.*

Six larval stages can be distinguished in the course of the development, four Zoea stages, a Glaucothoë, and a group of adolescent stages. The Zoeas of *Eupagurus* are very characteristic and can be picked out by the unaided eye in a miscellaneous assemblage of small Crustacea by their shape alone. The carapace is large and free from carinae or spines. It is excavated, not deeply, at the back, and as a result there are two latero-posterior, prominent pointed projections, which, however, are never prolonged into spines.

* *Proc. Boston Soc. Nat. Hist.* vol. XXXI., No. 4, p. 147.

The rostrum is fairly long and pointed. The whole carapace is smooth and quite free from minute denticulations. Each abdominal segment has two small dorsal and four lateral projections (two on each side) on its hind border. There are two fixed telson spines* on either side, the inner one straight and spinose, the outer smooth and curved, and a number of other spines, according to the age of the larva. A small hair-like process springs from under the outside spine on each side. The telson is a very characteristic spatulate shape with a median marginal notch in its posterior edge. There is a characteristic and obvious difference between the telson of this species (*E. bernhardus*) and that of the nearly allied *E. prideauxii* (figs. 48 and 49). The telson of *E. prideauxii* is shorter and more triangular in the first Zoea stage than that of *E. bernhardus*, but a more striking divergence is seen in the spines on the telson. The first Zoea of *E. bernhardus* has altogether six spines on either side of the median notch, and the third from the outside has no suture between it and the telson, and is half as long again as the inside spines. The same spine in *E. prideauxii* is equal in length to the other spines and is jointed to the telson. The proportion of length holds good through all the stages. The uropods of the later stages also differ. The living Zoea is transparent and has a patch of reddish yellow pigment under the dorsal side of the carapace. The eyes are compound and black, with a narrow yellow surround; two red spots are often present under the eyes on the mouth region.

The six larval stages may be distinguished by the following characters:—

* i.e., spines which do not articulate with the telson.

First Zoea.*—The first and second maxillipedes are developed and their exopods bear four feathered setae (fig. 56, Pl. VI). No thoracic limbs are present. The telson has four articulated and two telson spines on either side of the median notch (fig. 48). Only five abdominal segments can be distinguished, the sixth is fused with the telson.

Second Zoea.—Three maxillipedes are present and the rudiments of the thoracic limbs have appeared. Exopods of maxillipedes have six setae. The "anlagen" of the uropods present in early stages, and in late ones the rudiments of the limbs may be seen through the integument. Two extra spines appear on the telson (fig. 51).

Third Zoea.—The exopods of the maxillipedes have seven or eight setae and the uropods are present. The sixth segment of the abdomen is distinct. Gill rudiments are present on the limbs.

Fourth Zoea (Metazoea) (fig. 47).—The thoracic limbs are quite distinct and the fifth pereiopod, which is tucked up under the body, is chelate (fig. 50). The chelipedes are unequal. Rudimentary pleopods are present.

In organisation the Zoea stages do not differ from the others of their type among the Brachyura and Macrura, but in the next stage a complete metamorphosis is undergone and the great modifications in the structure of the adult Hermit Crab make their appearance.

The Glaucothoë was for a long time ranked as a distinct species of animal, chiefly because of its comparative scarcity. The scarcity was only apparent, however, because of the habits of the animal, and when

* Figures of the Zoeas and Glaucothoë of *E. longicarpus* may be found in Thompson's valuable paper (quoted above) and in: Faxon, Embryological Monographs, 1. Crustacea. *Mem. Mus. Comp. Zool.*, Harvard, Vol. IX, No. 1, 1882.

a suitable time and method for catching them is chosen, they can be obtained in large numbers. Like the fresh-water Mysis, they spend the day at the bottom of the sea and rise to the surface at night. The Glaucothoë has a carapace, of adult shape, but the branchiostegite is not bent down at right angles to the cephalic shield. Pleopods are present on all but the first abdominal somite, and the right uropod is smaller than the left. The otocysts have now appeared. It is during this stage that the animal first seeks a moveable residence and the larvae spend their time in alternately prowling on the bottom and swimming about. The stage usually lasts four or five days, and in that period the livers, excretory bladder and gonadial organs shift to the abdomen, while the more superficial structures undergo degeneration. The abdominal muscles become modified, the right pleopods disappear, and those on the left side degenerate. The metamorphosis is not dependent on a body covering, but completes itself even if the animal is kept naked, although the stage lasts much longer (up to six or eight days) and the mortality is very high.

"The anatomical modifications that appear during the Glaucothoë stage are, with but one exception, uninfluenced by either the presence, absence or form of the shell. The exception is found in the retention of rudimentary pleopods on the right side of the body in the sixth stage, though typically at this period appendages should be absent from this side."—(Thompson.)

Adolescent phase.—In this stage the typical adult structure is attained. The organs develop completely and the pleopods definitely show the sex of the animal, but Thompson finds that sexual maturity is not reached till a year or more after the moult from the Glaucothoë stage to the young adult,

The hermit crab has suffered from the neglect so commonly meted out by competent zoologists to animals whose peculiar habits have attracted the attention of the unscientific observer. There is consequently a large mass of undigested facts and fables concerned with its mode of life and habits, and an equal paucity of accurate morphological data. The most remarkable precocity has been attributed to this creature, with no regard for the comparatively lowly position it fills in the animal series.

I have not come across many early references to the hermit crab. Aristotle notices two species—probably *E. bernhardus* and *Diogenes varians*—briefly and indifferently well. He found them in the shells of Strombus, and remarks on the softness of the exoskeleton, the fact that they are not attached to the shell they occupy but change as they outgrow it, their possession of an oesophagus which leads into a stomach—there is no recognition of a gut or an anus—and finally, the astonishing statement that some anomuran, it is not clear which, casts a web across the mouth of its habitation to capture its prey. He considered these animals to be intermediate between the Mollusca and Crustacea, and that they originated, like the former group, from mud and sand.

Swammerdam (1738) was the first to make a scientific investigation of the hermit crab's anatomy, and except for one terrible mistake (referred to below) his work was very advanced. The account of the nervous system is especially good, and his careful dissection prevented him falling into the serious errors committed by Gegenbaur and Claus, among others, which have found their way into modern text-books,

Its Habitation.

The possession of a shell of foreign origin has probably had more share in attracting the attention of naturalists to the hermit crab than any other of its habits. The tenant's right of ownership was the chief problem. Swammerdam went so far as to argue that the shell was actually secreted by the inmate, and supported his contention by various ingenious arguments. Later observers took the less charitable but, unfortunately for the animal's reputation, the more tenable view that the shell had been obtained from a friendly or perhaps a much wronged Gastropod Mollusc. Whether the crab had simply appropriated the vacant home of a deceased whelk, or whether it had forcibly ejected the owner of the shell—added "murder to piracy"—was the question to be decided.

Bell argued from the fresh and clean shells in which hermits are frequently lodged that they attack the living mollusc and eat it out of its home. In fact, he considered that they are designed to keep the mollusc population in check. This idea seems to be strengthened by the fact that fishermen sometimes trawl the animals in the act of eating the whelk from its shell, presumably in anticipation of using it for a covering. Bell's argument and the fishermen's observation are quite accurate, but they do not prove that the hermit crab attacks the living Gastropod. In the first place it is not very conceivable that a hermit crab would have the strength to remove bodily, or the appetite to devour, an extremely tough animal like the whelk. Such an objection, however, does nothing to elucidate the facts which have been stated, but I think the following suggestion will go a long way towards meeting them.

It is well-known that the cod feeds very largely on the whelk, and that nothing but the operculum is ever found in the fish's stomach. The mollusc's fleshy portion (chiefly the foot and head) must therefore be bitten off while expanded—a comparatively simple matter to the active and powerful Teleost—leaving the softer (visceral) parts inside the shell. There is no doubt that the hermit crabs might then eat out these softer parts, and afterwards ensconce themselves in the new shell. I do not wish to imply any necessary connection between the adoption of a new shell and the emptying of its contents; in fact my observations all go to show that the crab will accept any covering rather than delay to clean a shell, let alone wait to dine off the contents. Thompson's experiments have led him to the same conclusion.

Choice of Shell.

The young Eupagurids have a much larger field of choice in the species of shell they inhabit than their elders have, and in addition the young whelks and other small Gastropods have many more enemies than the more powerful adult whelks. The full-grown *Eupagurus bernhardus* always seems to prefer the shells of *Buccinum undatum* (the common whelk), and *Fusus antiquus* (the hard whelk), above all others for a home; in fact, his bulk at maturity leaves him little choice. Among the many score of specimens I have examined, only two were in other shells, and each of these had chosen a very large example of *Natica nitida* for his abode. *E. prideauxii* is much less fastidious in its choice of a house than its martial brother, owing partly to the fact that the animal never attains the same size when fully grown, but still more to the investing anemone which

makes the possession of a full-sized shell of secondary importance. The young *E. bernhardus* is able to select from a large number of species. I have found specimens commonly in the following, but they use almost any shell or hollow object of suitable size and shape.

Buccinum undatum (young).	Littorina littorea.
Fusus antiquus (young).	Dentalium entale (rarely).
Murex erinaceus (young).	Purpura lapillus.
Natica nitida.	Trochus cinerarius.
N. monilifera.	Nassa incrassata.
	Turritella communis.

Biology of the Shell.

The possession of a shell is a matter of importance to the hermit crab, not solely for its protective value, but also because it seems to concern its health. Although crabs may be kept naked for a considerable time if they are solitary and in suitably inoffensive surroundings, they weaken in time and eventually die. To keep them without covering in company, or with rough and jagged surroundings, is rapidly fatal, as the delicate abdomen is very easily ruptured, and death invariably follows. M. T. Thompson has experimentally studied the effect of the shell on the metamorphosis, with valuable results. His conclusion is: "The stimulus of a shell is not necessary for the completion of the metamorphosis any more than for its inauguration," but the change from the Glaucothoë to the adult is delayed on the average by the absence of a shell, and the health of the larva is deeply affected. His experiments on naked larvae show most distressing mortality. The shape and nature of the covering seems to matter little, either in respect of form or health, so long as one is present.

It is almost impossible to describe the crab's manner of vaulting into its shell. Its humour can only be appreciated by one who has seen it and can contrast the animal's previous nervous anxiety (Taylor uses the apt simile "A bather whose clothes have been stolen!") with its sleek impudence on safely reaching the desired covering.

The crab is extremely difficult to remove from its shell. Even if it is prevented from using the telson and uropods it will hold on quite effectually by flexing its abdomen strongly and elevating itself by its last two pereiopods against the roof of the aperture. The best way of getting it out of the shell is to break away the opening till the front of the animal is exposed, and then to insert a seeker and gently tickle the abdomen. The crab usually makes a rapid egress without rendering further resource to the bone-forceps necessary. Any other mode of removing it, apart from entirely breaking up the shell, is useless and generally ends in the parting of abdomen from thorax. Nevertheless their fellow hermits are sometimes able to do what man finds beyond his powers. The whole battle seems to lie in a sudden and unexpected onslaught, for if the crab has any suspicion of foul play it will not venture outside the inner whorls of its house; no further, in fact, than where it can still retain a firm hold.

In spite of the cumbersome shell the hermit crab is very nimble in its actions. I have seen individuals climbing steep faces of rock—the shell pendant behind them—which would have presented difficulty to a less severely handicapped crustacean.

The inside of the shell is kept aerated by means of the current of water from the branchial chamber, aided by the pleopods which lazily flap to and fro while the

animal is resting. The fact that *Anomia* is found quite far back in the shell, and that various small animals live in the last whorls of it, shows that the water must be fairly fresh.

It is not known how the faeces are disposed of. Possibly there is not enough waste matter to cause any serious nuisance, and the small Amphipods in the shell might conceivably remove some of its objectionable features.

Dr. Gray* long ago made the curious observation that hermit crabs have the power of dissolving the shells in which they live. He says that the lip and pillar on the inside of the mouth is often destroyed in the shells inhabited by this animal. It seems more probable that a partiality for old shells on the part of the crustacean, or a local scarcity of suitable shells, accounts for the fact. It is very unlikely that any "faculty for dissolving shells" is possessed by the hermit crab. The roughening of the internal surface he remarks on is caused by the scraping of the uropods and pereiopods.

Its Food.

The Hermit Crab is an omnivorous feeder. In its early youth it follows the cannibalistic instincts of other Zoeas, but the adult seems to be purely a scavenger. It will accept almost any animal or vegetable food. The left chela is almost invariably used for carrying the food to the foot-jaws and it also aids them in tearing the morsels to suitable shreds. It may be observed very frequently tossing sand with the same appendage between the mouth parts, and letting the grains drop as it rubs

* *Ann. & Mag. Nat. Hist.*, ser. 3, vol. 2, p. 164, 1858.

them. There is no doubt M. T. Thompson is right in thinking that the diatoms and foraminifera which are found in the alimentary canal come from this source.

Commensals.

Although *E. bernhardus* does not exhibit such apt illustrations of commensalism as some of its allies, it usually contrives to entertain some stranger in its abode. To the human observer, however, it has seemed less happy in its bargains than they. The Polychaet worm *Nereis* (*Nereilepas*) *fucata* is found in many shells. J. Hornell* states that 90 per cent. of the shells which have been taken possession of by hermit crabs contain the worm, but my records—made from the examination of a large amount of material—show that in not 30 per cent. were these animals found associated. The frequency of this case of commensalism on the South Coast is evinced by Gosse's observation that the fishermen of Weymouth are accustomed to break open the hermit crab's shells for the sake of the worm inside.

The Nereis usually remains out of sight in the back whorls of the shell, but it appears at meal times, thrusting its head out between the crab's foot-jaws to appropriate the very morsel on which its host is engaged. In several young crabs' shells (Littorina and Natica) I found young *N. fucata*, about half an inch in length. It would seem, therefore, that the worm changes house with its host as both grow up. It is difficult to suggest any advantage that the hermit crab can gain from the presence of this guest.

E. bernhardus is also found associated, but not in the L.M.B.C. district, with the sea-anemone *Sagartia parasitica*. It carries the coelenterate turretwise on top

* Fauna of Liverpool Bay, Rep. III. *L.M.B.C.* 1892, p. 126.

of its shell, in a manner most strikingly unlike the relations of its near ally *E. prideauxii* to *Adamsia palliata.* Here again the soldier crab seems to have been unfortunate in its choice of a partner, for the gain, as in the case of the Nereid, seems to be entirely on the side of the anemone. I have found one specimen of *E. bernhardus* with *Adamsia palliata* attached to its shell. The *Adamsia* was spread, like a table-napkin, over the lip of a full-grown whelk shell, making a sort of cushion for the crab to rest upon.

Not infrequently specimens are found—chiefly in shallow water—whose shells are covered with a colony of *Hydractinia echinata.* In some districts over 50 per cent. of the shells have this growth upon them; in others, specimens with it are infrequently obtained. Henderson* records rare instances of *H. echinata* being found along with *E. pubescens.* A combination which less frequently occurs is that of *E. bernhardus* with the sponge *Hymeniacidon suberea.* Only young specimens seem to carry the sponge, and the occurrence of the combination is most sporadic. Off Port Erin a haul of the dredge will sometimes be taken in which nearly every *E. bernhardus* is associated with this slimy red sponge.

There are other animals which are present in or on the shells inhabited by the soldier crab which are more casual than those which have been cited, and which come more strictly under the head of chance association than commensalism. The frequent presence on the shell of tube-building worms, and in the shell of the mollusc Anomia, Amphipods, and small crabs, are cases in point.

Pomatoceros is found both inside and outside the

* Decapod and Schizopod Crust. of Firth of Clyde. *Trans. Glasgow Nat. Hist. Soc.* 1886.

shells. I came across one specimen which had completely encircled the abdomen of its host in such a manner that the crab could not have moved without breaking the tube—a proof of either Crustacean idleness or Vermian hustle.

The Amphipod *Podoceropsis excavata* almost invariably infests the dirt at the bottom of the shells. A small crab which is not infrequently found with the Amphipod is the marble crab *Porcellana longicornis.*

Although this memoir is principally concerned with *E. bernhardus*, it will be of interest, while considering the commensals of the animal, to mention briefly some striking examples of the same phenomenon amongst other Pagurids.

One of the most familiar is the association of *E. prideauxii* with *Adamsia palliata*,* a well-nigh perfect example of its class from the naturalist's point of view. When the crab reaches a certain size it ceases to change its shell frequently, but relies more and more on the covering afforded by the anemone. It comes finally, in some cases, to use the shell only as a grip for the telson, or even to discard it altogether. The anemone often secretes a membrane of hardened mucus, continuing the mouth of the shell outwards, which forms a complete investment for the crab and a definite support for the anemone. It is not probable that any absorption of the shell by the anemone can take place. It is now well established that this hermit crab achieves the apparently impossible by transplanting the anemone when it changes its shell. Gosse was the first to see the feat accomplished, and he gives a faithful account

* For an excellent discussion of the relations between these forms and further details, see L. Faurot, in *Arch. Zool. expér et gén.* Paris, ser. 5, V, 1910, p. 421.

of the proceeding in his quaint "Year at the Sea-side,"* The crab and the Adamsia are never found separated from one another, and their mutual companionship seems necessary for their existence.

A similar but even more remarkable case of commensalism is that recorded by Alcock† between *Chlaenopagurus*‡ and a compound colony of Zoantharian polyps. The Actinian settles directly on the abdomen of its host, and grows over it imbedded in a copious fleshy coenosarc which the crab can draw over its head or throw back at will. There is no intermediate structure, such as the molluscan shell of *E. prideauxii*, to introduce the two forms. The crab simply pulls the coenosarc over its back like a cloak, and keeps it in position with his claws—"the polyps seeming to have no power of adhesion."

A nearer approach to the method adopted by Adamsia is seen in *Parapagurus pilosimanus*, which lives in the cavity in the coenosarc of a large Epizoanthus which had settled originally on the shell of the hermit crab, but had absorbed it on growing up. Other associations with Actinians are seen in *Pagurus striatus* and *E. excavatus* with the anemone *Sagartia parasitica*. *P. striatus* plants the anemone (which however, is independent of the association for its existence) on its shell in much the same fashion as *E. prideauxii* does the Adamsia, *i.e.*, by means of its chelae. The two species are often found living separately, and *P. striatus* does not confine its attention strictly to Sagartia.

* An interesting but highly coloured note on the habits of this pair by Stuart Wortley may be found in *Ann. & Mag. Nat. Hist.* ser 3. XII. p. 388, 1863.

† *Journ. Asiatic Soc.* Bengal. Pt. II., No. 2, 1899.

‡ This species is now included in Henderson's *Paguropsis*.

Besides the Hymeniacidon occasionally found with *E. bernhardus*, a species of Suberites (probably *S. domuncula*) not infrequently occurs in connection with *E. pubescens*. The sponge often completely absorbs the original shell of the hermit crab, leaving the crustacean in a smooth cavity in its interior. This crab is also found with the same Hymeniacidon which has already been mentioned in connection with *E. bernhardus*.

Some tropical forms which utilise the cavities found in corals and sponges can hardly be included under this section.

PARASITES.

I have found no internal parasites in the species under consideration, and I do not believe any have been recorded. Three external parasites are known. In the branchial chamber the Isopod *Bopyrus* is found, and on the abdomen *Phryxus paguri* and the degenerate Cirripede *Peltogaster paguri*.

As the last-named parasite has a remarkable and well-known effect on the generative organs of its host, it might be useful to summarise briefly the results of investigations which have been made on the subject.*

The infection by Peltogaster has the immediate effect of diminishing the size of the gonads, and at an early stage ova make their appearance in the glandular part of the testis. The male secondary sexual characters are stimulated to development towards the female type, and if the female is infected early a retarding influence is exerted by the parasite on its attainment of sexual characters. If the parasite be extirpated the modifica-

* F. A. Potts. *Q.J.M.S.*, Vol. L., pt. 4, Nov. 1906, p. 599.

tions caused by it are retained. The changes are probably not due to the direct action of the Peltogaster, but are rather attributable to some change in the general metabolism caused by the parasite.

ECONOMICS.

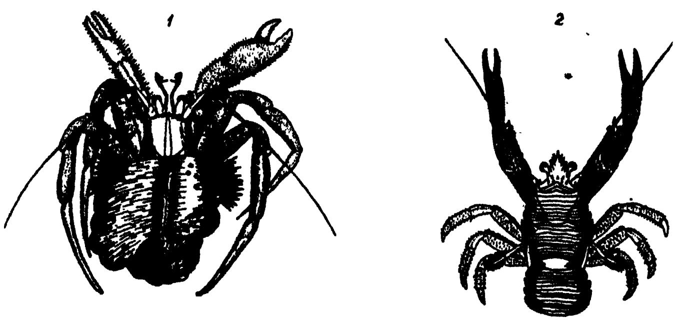
The economic value of the hermit crabs, so far as their direct use to man is concerned, is almost negligible. Indirectly they are of some value since they form the staple food of the larger fishes—the remains of *E. bernhardus* are familiar objects among their stomach contents—and on some parts of the coast they are used by fishermen to bait their lines. Bell in his "British Stalk-eyed Crustacea" (1853) says, "The Hermit Crabs are much employed by the fishermen (who call them 'Wigs,' or possibly 'Whigs') as bait for cod; for which purpose they answer very well for immediate use, although the original possessors and builders of the house, the whelks, are much preferred for night-lines as remaining more firmly on the hook. They are taken in great numbers in prawn-pots for this purpose." This remark holds equally well at the present day.

Even now, for example, the fishermen of Port Erin make considerable use of hermit crabs during the winter, as bait for cod, ling, skate and other fish on their long lines. This is not a usual practice on the Lancashire coast, and the men do not bait with the crabs unless there is a deficiency of whelks, owing, they say, to the fact that the whelks remain longer on the hook.

At Port Erin the crabs are caught in the whelk pots, and are used along with the whelks as bait, but some of the men declare that the hermits are "the very best bait you can get for cod; none better!" When

preparing the bait the man cracks the whelk shell with a slight blow from a stone or hammer, picks out the hermit and pulls the body apart at the peduncle or between the last two thoracic segments. The cephalothorax and its appendages are thrown away, and the soft abdomen only is put on the hook. The custom in Devon of breaking the shell to extract the Nereis within has already been referred to (p. 66).

Only one species seems to be used as food by the human race. The natives of the Islands of the Pacific, on which *Birgus latro*—the famous cocoanut crab—occurs, greatly prize the oily abdomen of the beast as a gastronomic delicacy.* The British Pagurids are not sufficiently common ever to be exploited commercially as a food for the table, but there seems no reason why such a clean and dry Crustacean should not make as delectable a dish as its more favoured Macrurid and Brachyurid relations.



ANOMURA.

* I have since seen an early description (*Zool. Journ.* 1828) of the habits of Coenobita in Jamaica, in which it is stated that the natives habitually bake the crab in its shell, and the author assures us it is quite a savoury dish thus prepared. It is still eaten largely on that island.

Note on the Structure of the Eye.

Since this Memoir was put in type, I have seen a recent paper by Dr. E. Trojan on "Das Auge von Palaemon squilla" (Denk. d. Math. Naturwiss. Klasse d. K. Akad. d. Wiss. Wien, Bd. 88, 1912).

The following are the most interesting points in it:—He agrees with Parker that there are only two corneal cells. They are broader distally than proximally, so that they appear triangular in transverse section. The crystalline cells are abruptly cone-shaped distally, and pass between the corneal cells to the facet: he confirms Parker in regard to their general structure.

The general structure of the retinular cells and rhabdome is as Parker and later writers have described, but he supports Hesse's opinion (and differs from Parker and Schneider) that there is no "zwischensubstanz" between the "stiftchen" composing each half-plate of the rhabdome. Three optic ganglia are described.

The most important part of the paper is devoted to a study of the pigment of the eye in darkness and light; this, however, is best consulted in the original. The author states that there are only two pigment-bearing cells, which form a continuous tubular sheath enclosing the whole ommatidium, and believes this to be the case for all Decapods. Parker's statement that the retinular cells and tapetum (accessory) cells are pigmented, is, therefore, possibly erroneous. The paper is illustrated by most beautiful plates.

EXPLANATION OF PLATES.

Reference Letters.

A.

A_1 = First antenna.
$A._1$ *a.* = Articular cavity of first antenna.
$A._2$ = Second antenna.
$A._2$ *a.* = Articular cavity of second antenna.
ant. a. = Antennary or lateral artery.
ant. p. = Anterior fold of oesophagus.
asc. a. = Ascending arterioles.

B.

bl. = Abdominal bladder or nephrosac.
bl. c. = Ducts between anterior and posterior vesicular mass.
b. m. = Basement membrane.
bp. = Basipodite.

C.

caec. = Abdominal caecum.
car. = Cardiac foregut.
c. hy. = Corneal hypodermis.
cm. = Oesophageal commissures.
cm. ab. = Abdominal commissures.
c. o. = Cardiac ossicle
cor. = Cornea.
cp. = Carpopodite.
cp. v. = Cardiopyloric valve.
cu. = Cuticle.
cx. = Coxopodite.

D.

d. c. = Dorsal coil of vas deferens.
d. liv. = Ducts of liver.
dp. = Dactylopodite.
d. re. = Distal retinular cells.
d. st. a. = Descending sternal artery.

E.

end. = Endopodite.
eg. l. = Epigastric lobe.
ep. = Epimera.
epl. = Endopleurite.
e.s. = Cells lining the endsac.
est. = Endosternite.
ex. = Exopodite.
ex. ap. = External excretory opening.
ex. op. = Aperture of otocyst.

F.

f. c. = Fat cells.
fl. = Flagellum.
fl. m. = Flexor muscles.
fm. c. = Ferment cells.

G.

$g._2$—$g._6$ = Abdominal ganglia.
g. g. = Green gland.
gl. = Rosette gland.
g. t. = Germinal tubule of testis.

H.

hep. a. = Hepatic artery.
h. g. = Hind gut.
hg. ep. = Epithelium of rectum.
hg. m. = Muscles of rectum.
ht. = Heart.

I.

inf. m. a. = Infra muscular branch of segmental artery.
int. = Intestine.
ip. = Ischiopodite.
i. v. = Inferior valve.

L.

lb. = Cells lining labyrinth.
l. liv. = Left lobe of digestive gland.
l. ov. = Blood vessels to left ovary.
l. p. = Lateral fold of oesophagus.
lt. = Lateral teeth.
lu. = Lumen of oesophagus.

M.

md. = Mandible.
md. a. = Artery to mandible.
m. g. = Mid-gut.
mg. caec. = Paired mid-gut (pyloric caeca).
mp. = Meropodite.
mt. = Median tooth.
m.v. = Median valve.
m. v. l. = Median ventral lobe.
mx. a. = Articular cavity of maxillae.
mx.a.′, a.″, a.‴ = Arteries to maxillae.
mxp. = Maxillipede.
mxp.a.′, a.″, a.‴ = Arteries to maxillipedes.
mxp.a. = Articular cavity of maxillipedes.

N.

n. a.$_1$ = Antennulary nerve.
n. a.$_2$ = Antennary nerve.
n. av. = Otic (Static) nerve.
n. fib. = Nerve fibrillae.
n. md. = Mandibular nerve.
n. md. m. = Mandible muscle nerve.
n. m. o. = Optic motor nerve.
n. mx.′, *n. mx.″* = Nerves to maxillae.
n. mxp.′, *mxp.″*, *mxp.‴* = Nerves to maxillipedes.
n. op. = Optic nerve.
n. op. f. = Optic nerve fibres.
n. p.$_1$—*n. p.*$_5$ = Nerves to pereiopods.
n. pl.$_1$—*n. pl.*$_4$ = Nerves to pleopods.
n. po. = Post-oesophageal nerve.
n. r. = Nerve branches on rectum.
n. teg. = Tegumentary nerve.
n. u. = Nerve of uropods.
nu. = Nucleus.

O.

oes. = Oesophagus.
op. a. = Articular cavity for eye.
opth. a. = Ophthalmic or median artery.

P.

p.$_1$ *a.*—*p.*$_5$ *a.* = Arteries to walking legs.
p. g. = Par-oesophageal ganglion.
pg. l. = Paragastric lobe.
plp. = Pleopod.
p. p. = Prepyloric ossicle.
prop. = Propodite.
prot. = Protopodite.
p. re. = Proximal retinular cells.
pt. = Pigment.
ptc. = Pterocardiac ossicle.
py. = Pyloric ossicle.
py. a. = Pyloric ampullae.
pyl. = Pyloric fore-gut.

R.

rb. = Rhabdome.
r. liv. = Right lobe of digestive gland.
r. ov. = Blood vessels to right ovary.

S.

s. abd. = Superior abdominal artery.
s. c. = Sternal canal.
sca. = Scaphognathite.
seg. a. = Segmental artery
sg. l. = Supragastric lobe.
smp. = Spermatophore.
sptd. = Spermatid.
sptc. = Spermatocyte.
spz. = Spermatozoa.
st. = "Stiftchen."
st. a. = Sternal artery.
stb$_1$ = "Stiftchen" bundles cut longitudinally.
stb$_2$ = "Stiftchen" bundles cut transversely.
st. bd. = Striated border.
st. g. = Stomatogastric ganglion.
st. n. = Stomatogastric nerve.
s. v. = Superior valve.

T.

T. = Telson.
tes. = Testes.
t. ex. ad. = Tendon of ext. add. mus. of mandible.
T. som. = Thoracic somite.
ts. t. = Glandular tube of testis.

U

uc. = Urocardiac ossicle.
ur. = Uropod.
ur. an. = "Anlagen" of uropods.

V.

v. d. = Vas deferens.
vit. = Vitrellae or cone cells.

Y.

y. c. = Young cell of digestive gland.

Z.

z. c. = Zygocardiac ossicle.

Roman numerals indicate thoracic somites in several figures.

Plate I.

Fig. A. *Eupagurus bernhardus* (male), viewed from the dorsal side. Natural size.

Fig. B. *E. bernhardus* (female), from the ventral side. The distal joints of the thoracic limbs have been removed and the mouth parts are not shown. The distortion of the sternal plates caused by the asymmetrical chelipedes can be seen. Natural size.

Fig. C. *E. bernhardus.* General view of the animal sitting in its usual posture in a shell of *Buccinum undatum.* Natural size.

Plate II.

Fig. 1. Left first antenna (antennule) from side. × 3.

Fig. 2. Left second antenna, from above. × 3.

Fig. 3. Left mandible, from below. × 4.

Fig. 4. Left first maxilla, from below. × 4.

Fig. 5. Left second maxilla and scaphognathite, from below. × 3.

Fig. 6. Left first maxillipede, from below. × 4.

Fig. 7. Left second maxillipede, from inner side. × 3.

Fig. 8. Left third maxillipede, from inner side. × 2·5.

Fig. 9. Dorsal side of right chela. × $\frac{4}{5}$.

Fig. 10. Left chela, from dorsal side. × $\frac{4}{5}$.

Fig. 11. Left third pereiopod, from front. × 1.

Fig. 12. Left fourth pereiopod, dorsal. × $2\frac{1}{4}$.

Fig. 13. Left fifth pereiopod, dorsal. × $1\frac{1}{4}$.

Fig. 14. First pleopod of female, dorsal. × $3\frac{1}{2}$.

Fig. 15. First pleopod of male, dorsal. × 4.

Fig. 16. Telson, uropods and last abdominal segment. × 3.

Plate III.

Fig. 17. Endophragmal system from the dorsal side. The carapace and tergum of the last thoracic somite have been removed and the soft parts cleared away. × $1\frac{1}{4}$.

Fig. 18. Endophragmal system. The plates in the fifth somite viewed from behind. × 2.

Fig. 19. Alimentary canal. Longitudinal section through stomach to show the skeletal structures. × $3\frac{1}{2}$.

Fig. 20. Diagrammatic trans. sect. of oesophagus to show glands and constricted lumen

Fig. 21. The stomach from the left side with the organs opening into it. × $2\frac{1}{2}$.

Fig. 22. Transverse section through rectum. × 350.

Fig. 23. Liver tubule in transverse section. × 103.

Fig. 24. "Ferment" cells of liver. × 556.

Fig. 25. Dissection from dorsal surface. The blood system of the dorsal side in front of the heart is shown. Vessels behind the heart have been removed. The left mid-gut caecum has been exposed and spread out. The lobes of the digestive gland have been separated to show the alimentary canal, and the left lobe has been turned over to show the testis imbedded in it. × $1\frac{1}{2}$.

Plate IV.

Fig. 26. The sternal artery and its branches from the dorsal side. The descending portion of the artery is turned to the right side. The vessels to the pereiopods have been cut short. × $1\frac{1}{2}$.

Fig. 27. Arterial system of the abdomen. The vessel *s. Abd.* runs on the surface of the liver, the vessel *seg. a.* underneath on the muscle.

Fig. 28. Heart, latero-dorsal view. × 6.

Fig. 29. Excretory system. The left epigastric lobe, all the other organs of body, the muscles and the abdomen have been removed. Semidiagrammatic. × 2.

Fig. 30. Second antenna from below to show the excretory orifice. × 3.

Fig. 31. Excretory system. Section of wall of nephrosac. × 290.

Fig. 32. Section of portion of antennary gland to show the cells of the endsac and labyrinth. × 180.

Fig. 33. The Eye. Longitudinal section (semi-diagrammatic) of an ommatidium, very greatly magnified (modified after Hesse and Schneider).

Fig. 34. The Eye. Diagram of a proximal retinular cell (modified after Parker).

Fig. 35. The left auditory sac (statocyst) with the surrounding tissues removed. The sac has been cut open from the dorsal surface to expose the sensory region. × ca. 23.

Fig. 36. Plumose seta from the statocyst, very greatly magnified.

PLATE V.

Fig. 37. Nervous system of the cephalothorax from above. The nerves have been cut short before they enter the appendages. × ca. $1\frac{1}{2}$.

Fig. 38. Nervous system. The abdominal ganglia and their connective and branches. × 2.

Fig. 39. The front of the stomach with the stomatogastric system of nerves. × 4.

Fig. 40. The right testis from above, with the vas deferens. × 2.

Fig. 41. Testis. A tubule in the region of the "dorsal coil" opened from the side. The chitinous tube of spermatozoa is seen to be partially divided up. × ca. 25.

Fig. 42. Testis. Spermatophores lower down the tube than in fig. 41. × ca. 50.

Fig. 43. A complete spermatophore at the end of the vas deferens, with a portion of its ribbon. × 123.

Fig. 44 (*a* and *b*). Spermatozoids, (*a*) from the side, (*b*) (after Retzius) from above.

Fig. 45. Section through glandular portion of testis. × 103.

Fig. 46. Section through germinal tubules containing free spermatozoa. × 103.

Plate VI.

Fig. 47. Fourth zoea of *Eupagurus bernhardus*, from the right side. × 16.

Fig. 48. Telson of first zoea of *E. bernhardus*. × 25.

Fig. 49. Telson of first zoea of *E. prideauxii*. × 25

Fig. 50. Chela of fourth zoea of *E. bernhardus*. × 35.

Fig. 51. Telson of second zoea of *E. bernhardus*, with "anlagen" of uropods. × 14.

Fig. 52. Tip of uropod of fourth zoea.

Fig. 53. Uropod of third zoea.

Fig. 54. First maxillipede of fourth zoea. × 50.

Fig. 55. Telson and uropods of fourth zoea. × 28.

Fig. 56. First maxillipede of first zoea. × 60.

Plate I.

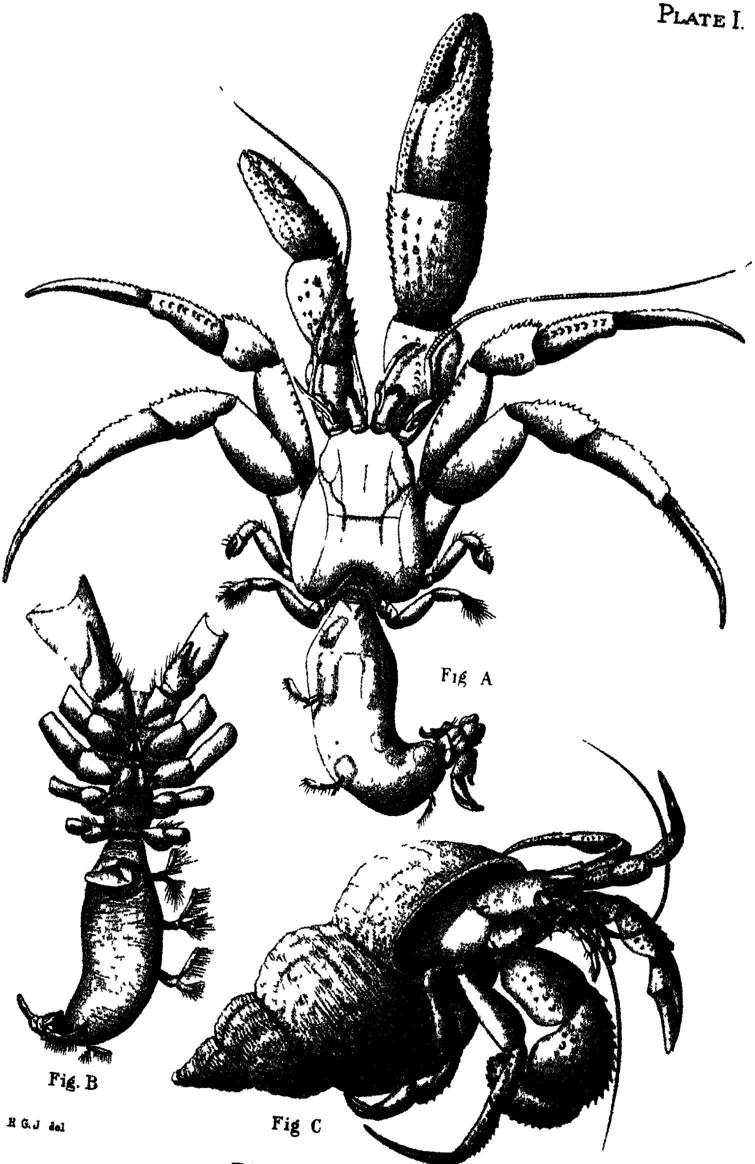


Fig A

Fig. B

Fig C

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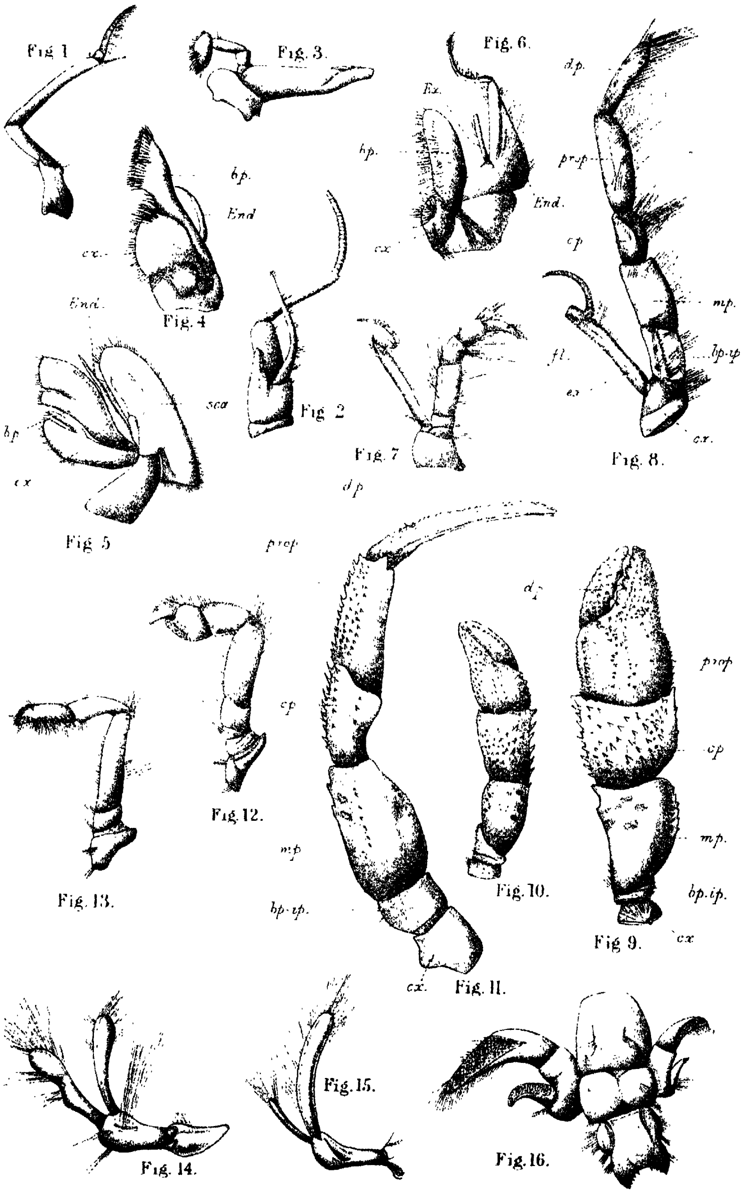

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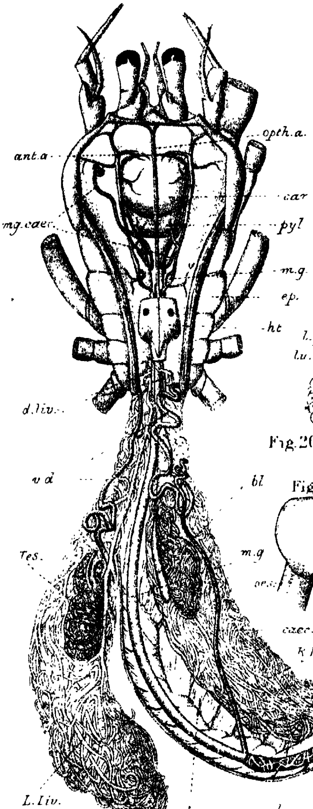

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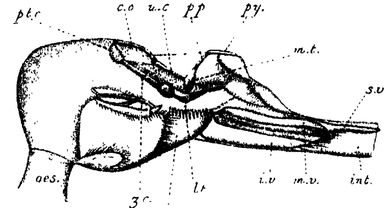

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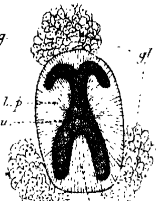

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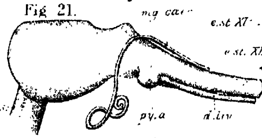

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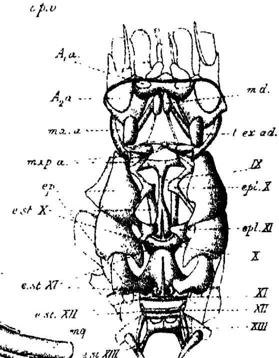

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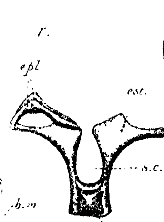

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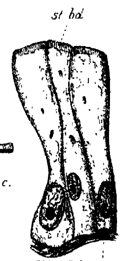

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Fig. 22.

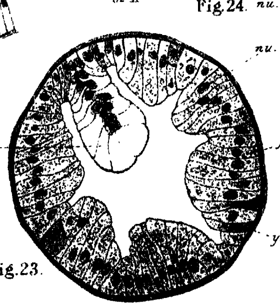

Fig. 23.

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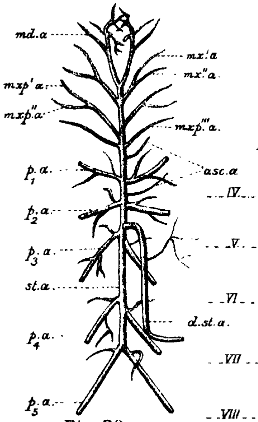

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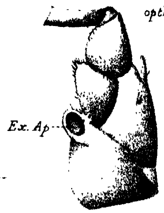

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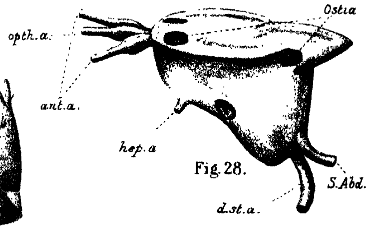

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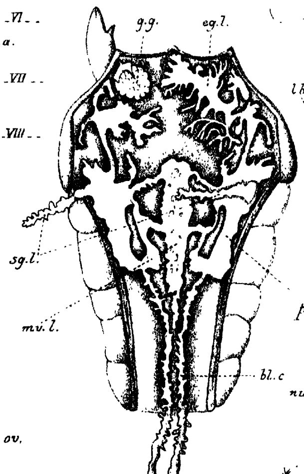
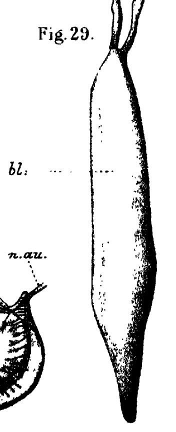

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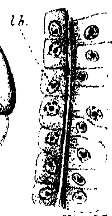

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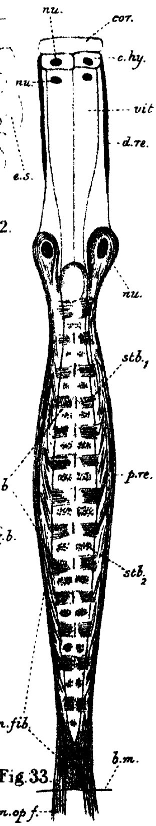

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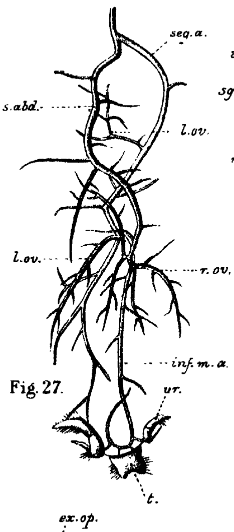

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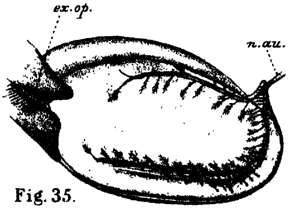

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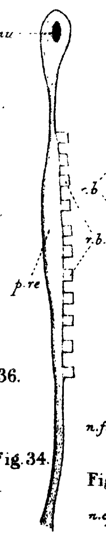

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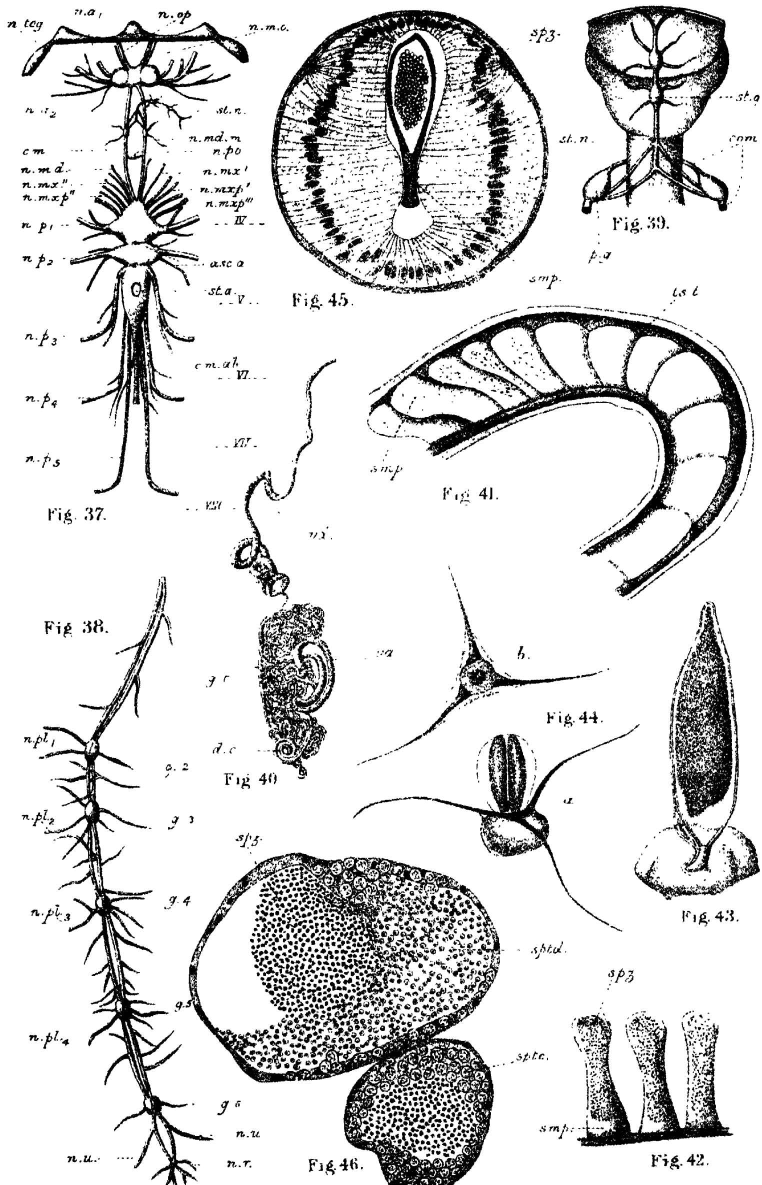

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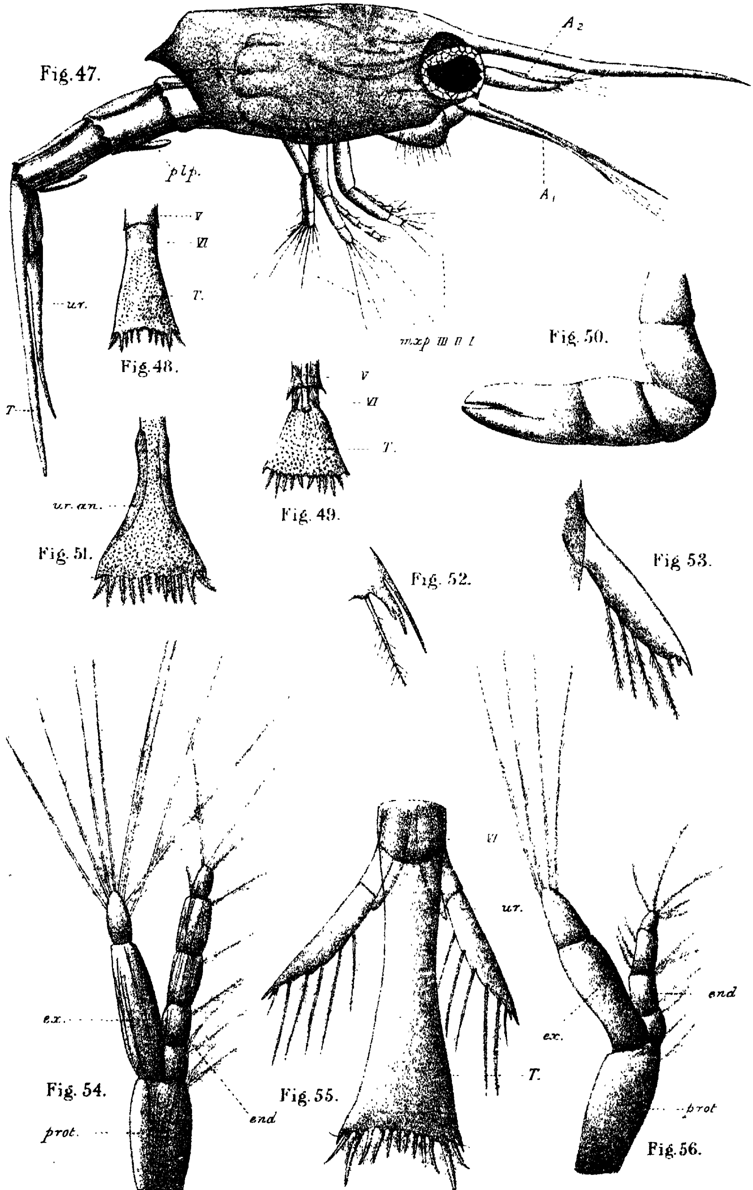

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